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TITLE: Brain Mechanisms of Affective Language Comprehension in Autism Spectrum Disorders

PRINCIPAL INVESTIGATOR: Dr. Donald Joseph Bolger

CONTRACTING ORGANIZATION: University of Maryland
College Park, MD 20742

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14. ABSTRACT
Profound deficits in the domain of social communication are a hallmark of autism spectrum disorders (ASD). These difficulties in social communication can have devastating effects for both individuals with autism and their loved ones as they negatively impact the ability to form and maintain relationships (Baron-Cohen, 1988; Dawson & Bernier, 2007). Difficulty understanding other's emotions is central to the socialcommunicative difficulties in ASD. Research suggests deficits in emotion processing are greatest in the perception and comprehension of other's emotions (e.g., Sigman et al., 1992; Losh and Capps, 2006). One mechanism by which comprehension of other's emotions is achieved is through the association of a verbal label or visual cue (e.g. facial expression) to one's own emotion during development. Failure to associate the appropriate label with the emotion may lead to difficulties inferring another person's emotions from context. Difficulties in emotion processing have been studied extensively in the visual domain through primarily perception of emotional expressions but relatively little is known about brain mechanisms underlying a failure to infer emotions from verbal context.

15. SUBJECT TERMS-

16. SECURITY CLASSIFICATION OF:			**17. LIMITATION OF ABSTRACT**	**18. NUMBER OF PAGES**	**19a. NAME OF RESPONSIBLE PERSON** USAMRMC
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1. **INTRODUCTION:** Narrative that briefly (one paragraph) describes the subject, purpose and scope of the research.

The project, Brain Mechanisms of Affective Language Comprehension in Autism Spectrum Disorders, is an investigation into the behavioral and biological bases of the social communication deficits in individual with autism spectrum disorders (ASD). Autism is characterized by impairments in both social interaction and language. While these domains are often studied separately, their interaction presents the greatest challenge to individuals with ASD. Effective social interactions depend on fluent and flexible language comprehension. An area of particular difficulty in ASD may be in the ability to comprehend the social or emotional content of the speaker's message. The primary goals of this project are to a) identify whether this comprehension deficit stems from failures in processing affect and meaning from individual emotion words or from a general difficulty in processing meaning from words with abstract referents; and b) whether the source of this deficit emerges from difficulties inferring emotional states from, largely social, contexts. Neuroimaging measures provide an objective measure of affective processing and provide insight into brain mechanisms underlying impaired affective comprehension. Functional MRI is currently being collected from typically developing young adults (18-24) and those with high-functioning autism during multiple experiments. In the study described in the proposal, social scenarios describing emotionally evocative situations will be presented auditorally in vignettes and then participants will be asked to respond about the protagonist's feelings with a congruent or incongruent emotional word: "He/She felt sad/happy."

2. **KEYWORDS:** Provide a brief list of keywords (limit to 20 words).

Affective Language, High functioning autism spectrum disorder, functional Magnetic Resonance Imaging (fMRI), Social-emotional processes, emotional inference task

3. ACCOMPLISHMENTS:

What were the major goals of the project?

Specific Aims 1a & 1b: ***Determine whether individuals with autism spectrum disorder fail to draw emotional inferences from linguistic contexts and whether these putative deficits are shown with respect to activation elicited in emotion processing regions of the brain.***	**Proposed Timeline**	**Completed**	**Accomplishments**
Major Task 1: Experimental Design	Months		
Subtask 1: Finalize the design for the research protocols and analysis to be performed in all years. This includes the development of protocols and behavioral and neural assessments. This task also includes any changes in design of fMRI tasks and scanning protocols as necessary. The design will remain constant throughout the duration of the project. Participating teams:	1-3	9/10/2015	Finalized scan parameters and tested experimental protocols in mock sessions.
Subtask 2: Submit documents for local IRB* review The teams will prepare and submit any revised protocol materials for human participants to the institutional review board (IRB) of the University of Maryland. The team will work with the IRB to expedite the review process and address any human subjects concerns.	1	10/21/2015	HRPO required changes to protocol approved by UMD IRB.
Subtask 3: Submit IRB approval and necessary documents for HRPO* review.	2-3	10/21/2015	HRPO approval: 11/4/2014 documented: 12/5/2014
*Milestone #1: HRPO** approval received*	2-3		
Major Task 2: Human Subject Experimentation.			
Subtask 3: Recruitment of Participants. • The team will create a recruitment protocol particularly for individuals with Autism Spectrum Disorder. The team will utilize database information from the Interactive Autism Network (IAN) as well as outreach to local organizations that support individuals and families with ASD.	3-6		

Subtask 4: Running of Participants • Participants will be recruited during the first year and processed per the approved protocol, including behavioral assessments and neuroimaging protocols. • Participants with ASD will be targeted in the early portion of the study. Age and gender matched controls will be targeted in the latter half of the study.	6-30	As of 9/15/2015 ~50% of target goal	15 participants in ASD group and 16 in Typical group completed
Subtask 5: Initial Analysis of behavioral and imaging data • Conduct analysis within groups to determine the neural response in TD individuals making emotional inferences from language context and whether individuals with ASD fail to so.	30	9/11/2015	Dissertation Completed by Dr. Lesley Sand
Milestone #2: Co-author manuscript on the underlying neural system in Typically developing individuals when making emotional inferences.	30-32	10/4/2015	Manuscript submitted to *NeuroImage*
Subtask 6: Full analysis of functional MRI data during EIT task • Conduct within subjects and group differences to determine whether individuals with ASD have aberrant neural activity relative to typical controls when making emotional inferences.	30		
Milestone #3: Co-author manuscript on group differences in fMRI activation between groups on the EIT task	32-36		
Specific Aims 2: *Determine whether functional connectivity between emotion and language regions is reduced in individuals with ASD during the EIT task and at rest.*	**Timeline 30-36**		
Major Task 3: Data analysis of functional connectivity data in fMRI.			
Subtask 7: Analysis of functional connectivity data during EIT task and resting state stages of fMRI.	30		
Milestone #4: Co-author manuscript on group differences in functional connectivity between groups on the EIT task and rsfMRI.	32-36		

What was accomplished under these goals?

For this reporting period describe: 1) major activities; 2) specific objectives; 3) significant results or key outcomes, including major findings, developments, or conclusions (both positive and negative); and/or 4) other achievements. Include a discussion of stated goals not met. Description shall include pertinent data and graphs in sufficient detail to explain any significant results achieved. A succinct description of the methodology used shall be provided. As the project progresses to completion, the emphasis in reporting in this section should shift from reporting activities to reporting accomplishments.

There were three major activities in the first year of the project: 1) the finalization of the protocol, 2) the approval of the protocol with local IRB and HRPO, and 3) the recruitment and running of participants through the approved protocol. The first objective of finalizing the protocol was completed simultaneously to the start of funding in September of 2014. All protocols were tested in mock sessions without active research participants to ensure a) the effectiveness of the experimental paradigm, b) the proper timing for execution of the experimentation, and c) the appropriate scanning protocols for functional and structural Magnetic Resonance Imaging (MRI). The second objective during this period was obtaining final approval from the local Institutional Review Board (University of Maryland) and the Department of the Army's Human Research Protection Office (HRPO). Through conversations with HRPO, we amended our protocols with our local IRB and received approval on October 21, 2014. Those documents were forwarded to HRPO and received verbal approval verbally on November 4, 2014 with final documentation received on December 5, 2014. The third objective was to begin the recruitment and running of Human participants. Our goal for Year 1 was to run a total of 20 participants (10 ASD and 10 typical controls). Our successful initial recruitment efforts were positive and led to being well ahead of schedule. By the end of Year 1, we had run 31 participants (15 ASD and 16 typical controls). However, we expect some attrition of data (~10%) due to particular phenomena such as head movement while scanning which distorts the data beyond repair. This is fairly common in patients such as those with ASD. Thus, we have met and surpassed all goals for Year 1.

The major achievements in the period with respect to deliverables are that the data were preliminarily analyzed as we initially proposed to do in month 30 (Year 3). A brief description of the methods is detailed below. This preliminary analysis was conducted as part of the doctoral dissertation of Dr. Lesley Sand on September 11, 2015. The dissertation is included as a deliverable in Appendix A. A second major achievement was that Milestone #2, a written manuscript of the effects of the experimental paradigm within neurological typical adults, was also completed and submitted for publication. The manuscript is included as Appendix B. This milestone was initially scheduled to occur in month 30-32 (Year 3). In sum, many of the major accomplishments scheduled to occur within Years 2-3 are well underway or completed.

Brief Overview

Autism Spectrum Disorders (ASD) are pervasive neurodevelopmental disorders characterized by difficulties in social interaction. One critical aspect of fluent social interactions is the ability to

comprehend others' emotional states through language context. ASD individuals have difficulty attributing emotional labels to pictures or sentences as well as reduced memory for emotional words as compared to typically developing peers. As depicted in Figure 1, the current investigation aims to identify the brain mechanisms underlying difficulties with emotional language processing in ASD.

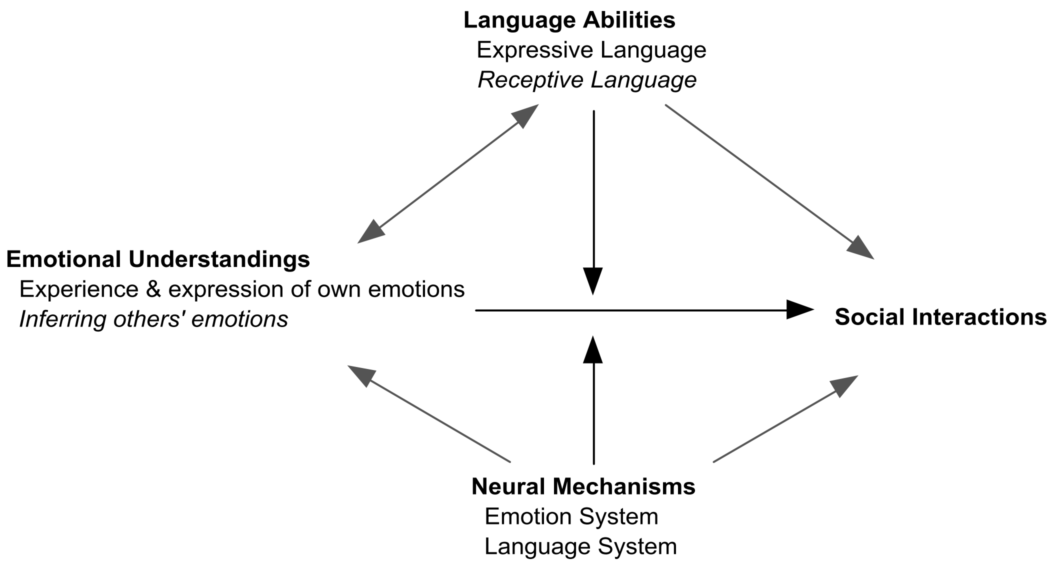

Figure. 1. Summary of mechanisms related to social interactions. The main focus of this research is the ability of individuals with ASD to infer others' emotions; this implies receptive language skills. However, emotional understandings include both one's own physical feelings and expressions of emotion as well as the ability to extend these understandings to others', and language skills include both expressive and receptive capacities. Neural systems related to both language- and emotion processes are well-defined, and impaired in autism.

Our hypothesis is that, unlike TD individuals, individuals with ASD, will not recruit emotion-related brain regions (e.g., the amygdala) while listening to stories with emotional content, suggesting a failure to elicit an appropriate emotional response to stories inferring others emotions. In the first year, we have collected functional and structural magnetic resonance imaging (MRI) data from 31 adolescents and young adults (16-30 years): 16 of whom are typically developing (TD) and 15 with ASD. Participants listened to stories in a task described below that required an emotional or neutral inference followed by a statement (e.g., "She felt [emotion]") for which they will be asked to make a congruity judgment based on the previous verbal context. Additionally, we predicted that ASD individuals will be less accurate in making congruity judgments about the emotion words (as compared to neutral words) and show reduced activation in regions involved in error monitoring during the presentation of emotion words that are incongruous to the sentence context. These findings would suggest that ASD individuals do not automatically associate a verbal label (e.g., 'panic') with context (e.g., sentence describing panic). Our second goal is to examine whether reduced task-based and resting functional connectivity between emotion and language-related brain regions contributes to these deficits in

making emotional inferences from language context. Findings from the current investigation will provide a greater understanding of the neural and cognitive mechanisms underlying difficulties with affective language processing in ASD individuals. Difficulties with understanding others' emotions through language negatively impact the formation and maintenance of close personal relationships in individuals with ASD. Findings from the current proposal can inform the development of more targeted interventions of emotional language comprehension to improve overall quality of life in individuals with ASD.

Methodology

We have developed an emotional inferences task (EIT) that enables us to use event-related fMRI to examine the cortical response to emotionally provocative situations presented verbally (short 12 second stories) and probes whether the participant recognizes the emotion that would be expected (*"He/She felt…"*). Validation of the EIT was done with 23 healthy adult participants revealing that stories with positive and negative emotional content engaged language and emotion centers of cortex relative to neutral stories matched on complexity. The EIT is well-suited for examining whether and how emotions are inferred from language using cortical measures.

Table 1			
Passage	Valence	Congruent Target	Incongruent Target
The woman could not get over the idea that her ex-boyfriend did not want to be with her anymore. Hearing that he was dating someone new made the situation even worse.	negative	She felt sad.	She felt happy.
The young man had waited so long for his favorite band to come to town that he could hardly sleep the night before the concert. He planned to arrive early to get autographs.	positive	He felt excited.	He felt disgust.
After the race, the jockey was covered head to toe, and he couldn't see through his goggles. Days of rain had saturated the track, so the horses kicked up great clods as they ran.	neutral	He felt dirty.	He felt clean.

Results

Neurotypical Adults

Our first objective was to ensure the effectiveness of our paradigm on neurotypical adults based on data collected prior to the funding period. Pilot data was provided in the proposal for funding and additional data was collected and analyzed prior to funding to enable us to complete Milestone #2. As shown in Figure 2, healthy adults show greater activation for emotionally valent stories (Panel B in red) in characteristic brain regions of social-emotional processing (See Appendix B for full results).

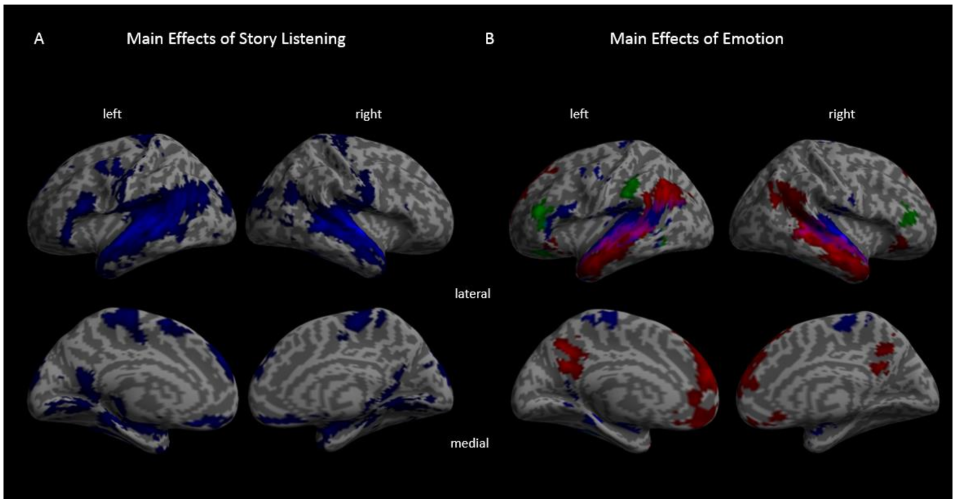

Figure 2. Activation maps illustrating the presence of significant functional activity associated with listening to stories. A) We show *t*-values for regions showing signal increases for the average effect of stories (positive + negative + neutral) vs. baseline contrast. B) We show *t*-values for signal increases associated with effect of emotion (positive + negative) vs. neutral in red, neutral vs. emotion in green, and neutral vs. baseline in blue. Regional variations in task-related activity are displayed using a threshold of $p < .001$ corrected with cluster extent FWE threshold ($p<0.05$) for t-statistic maps.

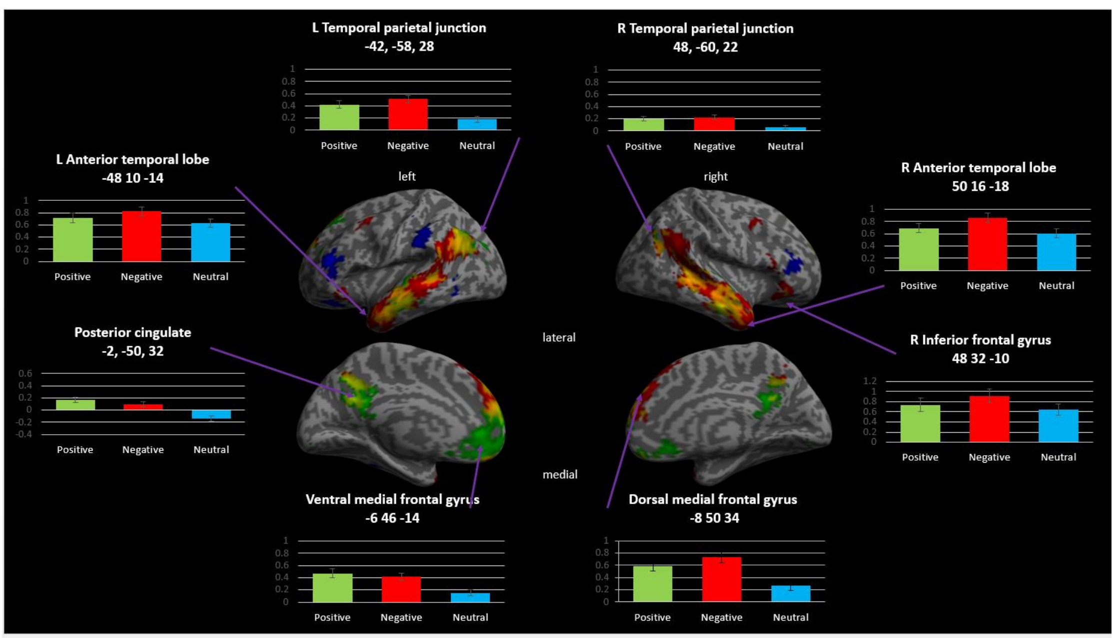

Figure 3. Activation maps illustrating the presence of significant functional activity associated with valence; effect of positive vs. neutral is shown in green, negative vs. neutral is shown in red, and neutral vs. emotion (positive + negative) is shown in blue. Yellow indicates areas of overlap. Regional variations in task-related activity are displayed using a threshold of $p < .001$ cluster corrected for t-statistic maps. Error bars show standard error.

The data were also analyzed to determine whether these effects were driven by positive or negative valent emotional inferences. Figure 3 displays the activation values in these regions as a function of the positive, negative or neutral valence of the stories that participants heard. Generally, greater activation to negative stories was found on the lateral surface of the brain.

Autism Spectrum Disorder

Having collected roughly half of the data for the current investigation, we conducted preliminary analyses as detailed as Subtask #5 for Human Experimentation. These analyses formulated the bases of the doctoral thesis for Dr. Sand as discussed the following results summarized here are in the thesis document in Appendix A.

The activation profile for emotionally valent stories in individuals with ASD looks remarkably similar to that of neurotypical adults as shown in Figure 4 below. The activation found in individuals with ASD was often greater than that for their typical peers. We identified the key regions of interest from our study above on typical adults that were indicative of social emotional processing. We then ran comparisons across those conditions between the participants with ASD and the typical controls. The resulting tests confirmed that there was greater activation in the social-emotional network in the brain for participants with ASD as shown in the bar graphs on Figure 5. However, there were no differences in other regions of general language processing that were engaged when listening to stories regardless of condition. The complete set of detailed results are in Appendix A.

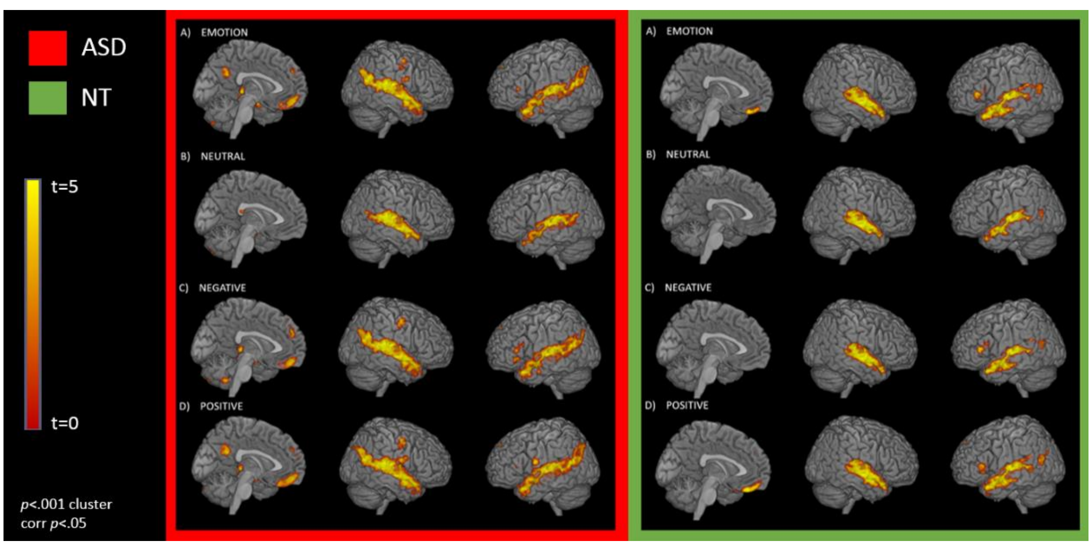

Figure 4. Within group comparisons, Study 2. (A) Contrast of emotion (A), neutral (B), negative (C) and positive (D) scenarios in autism (ASD; red), neurotypical (NT; green). Task-related activity is displayed using a cluster corrected threshold of $p < .001$.

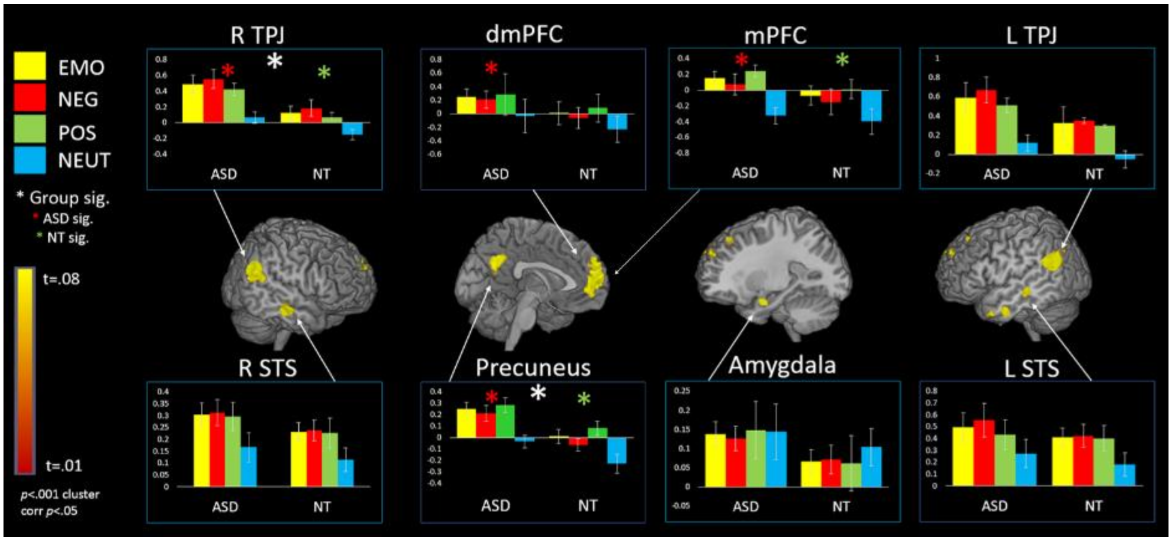

Figure 5. Regions of interest (ROI) from Sand (2015). Bar graphs show percent signal change in neural response to emotion (EMO; yellow), negative (NEG; red), positive (POS; green) and neutral (NEUT; blue) for individual ROI (*y*-axis), separated by autism (ASD) and neurotypical (NT) groups (*x*-axis). Error bars show standard error. * $p < .05$

Conclusions

With respect to our timeline and basic commitments, we have been generally successful in our accomplishing our goals well ahead of schedule. We have completed our preliminary study on healthy adults which has validated the experimental protocol that was proposed. We have successfully recruited and completed data collection on roughly 50% of our target number of human subjects for the sample of ASD and neurotypical peers. Preliminary analysis suggests that our protocol has been equally effective with our target population in eliciting neural responses.

The basic findings of this investigation to this point suggest that our initial hypotheses are not supported. That is, we predicted based on the previous literature of non-verbal emotion processing in ASD that these individuals would have underactivation of the regions of the brain associated with social-emotional processing. However, our preliminary results suggest that the inverse may be the case for verbal material. That is, when processing emotional content in language, participants with ASD may have fundamentally greater engagement of neural resources responsible for social-emotional processing.

At this point without a complete set of data, we are remiss to make strong conclusions. However, as we discuss in the document in Appendix A, there is a reasonable alternative hypothesis to why these results differ from our expected pattern. In general, these findings provide a substantial benefit to the scientific community if they remain after completion of the entire investigation.

What opportunities for training and professional development has the project provided?

Describe opportunities for training and professional development provided to anyone who worked on the project or anyone who was involved in the activities supported by the project. "Training" activities are those in which individuals with advanced professional skills and experience assist others in attaining greater proficiency. Training activities may include, for example, courses or one-on-one work with a mentor. "Professional development" activities result in increased knowledge or skill in one's area of expertise and may include workshops, conferences, seminars, study groups, and individual study. Include participation in conferences, workshops, and seminars not listed under major activities.

One of the largest benefactors from this project has been the training opportunities for graduate and undergraduate students that have had the opportunity to work directly on this investigation. As stated several places previously in this document, the preliminary analyses conducted for this project served as the basis for the doctoral dissertation of Dr. Lesley Sand who was the graduate student researcher funded on the grant in Year 1 and she will continue to serve as a post-doctoral researcher on the project through Years 2 and 3. Dr. Sand has worked closely over the course of this project with Drs. Bolger and Redcay in the preparation, data collection and data analysis as well as the manuscript and thesis writing involved for disseminating our findings. Dr. Sand has also attended a number of training workshops on special analysis techniques of MRI data using both Statistical Parametric Mapping (SPM) software as well as FreeSurfer, created by Harvard/Massachusetts General Hospital.

In addition to Dr. Sand, this grant has provided training opportunities for several undergraduates in the lab to learn about brain imaging and analysis of MRI datasets. These undergraduate students have received direct mentoring from Dr. Sand as well as Dr. Bolger meeting weekly with both researchers. One of those students, Ms. Laura Casey, is now attending a Masters Degree program in Cognitive Neuroscience at the University of Glasgow in Scotland. Two students, Solana Lazarte and Connor Laughland are still working on the project in the lab.

How were the results disseminated to communities of interest?

Currently, there are two means by which our findings have been disseminated:

The doctoral dissertation copyrighted by Dr. Sand and the University of Maryland (attached as Appendix A).
Sand, L. A. (2015). Neural Bases of Emotional Language Processing in Individuals with and without Autism. *Unpublished Doctoral Dissertation*, University of Maryland College Park. http://drum.lib.umd.edu/bitstream/handle/1903/17242/Sand_umd_0117E_16641.pdf?sequence=1

Manuscript submitted on Neurotypical adults to NeuroImage:
Sand, L.A., Redcay, E., Zeffiro, T. and Bolger, D.J. (manuscript submitted for publication). Neural Bases of Emotional Language Processing.

What do you plan to do during the next reporting period to accomplish the goals?

Describe briefly what you plan to do during the next reporting period to accomplish the goals and objectives.

Data Collection. During the next reporting period, we plan to continue data collection toward our goal of 30 reliable participants in each group (total of 60) with the expectation that some attrition will continue to occur. We expect to complete data collection between months 24-30 of the project.

Data Analysis. We will continue to analyze the current dataset with particular attention to the resting state functional connectivity (rs-fMRI) data that participants have contributed thus far. This data will enable us to examine the general connectivity of brain structures in our population of participants with ASD compared to our control sample with special interest in the regions engaged by our EIT paradigm.

Data Presentation. We will also prepare to present our preliminary findings of data at Scientific Meetings and Conferences such as the International Meeting for Autism Research (IMFAR) in May of 2016. In addition, the results will be discussed in seminars and colloquia by Dr. Bolger at other institutions such as Temple University and Penn State University in March of 2016.

4. IMPACT:

This component is used to describe ways in which the work, findings, and specific products of the project have had an impact during this reporting period. Describe distinctive contributions, major accomplishments, innovations, successes, or any change in practice or behavior that has come about as a result of the project relative to:

What was the impact on the development of the principal discipline(s) of the project?

Nothing to Report. *At this point of the project it is too early to have significant impact.*

What was the impact on other disciplines?

Nothing to Report.

What was the impact on technology transfer?

Nothing to Report.

What was the impact on society beyond science and technology?

Nothing to Report.

5. CHANGES/PROBLEMS:

Actual or anticipated problems or delays and actions or plans to resolve them

There are no problems to report at this time. The project is actually ahead of schedule.

Changes that had a significant impact on expenditures

Describe changes during the reporting period that may have had a significant impact on expenditures, for example, delays in hiring staff or favorable developments that enable meeting objectives at less cost than anticipated.

We have delayed in hiring a postdoctoral researcher in Year 1 on the project because Dr. Lesley Sand who was a senior doctoral student on the project was essentially equal to the task. Dr. Sand is now serving a postdoctoral researcher on the project and will continue to through Years 2 and 3.

Significant changes in use or care of human subjects, vertebrate animals, biohazards, and/or select agents

The only modification to the human subjects protocol were an addendum to the informed consent procedure that would allow the data to be shared in a data repository, the ABIDE database, for MRI of patients with Autism Spectrum Disorder.

The ABIDE dataset is a database of structural MRI and resting-state functional MRI scans as well as behavioral measures collected from children and adults with autism spectrum disorders and typically developing controls that multiple sites across the US (and some international) contribute data to. The goal is for researchers to be able to aggregate across sites with a sample much larger than is possible with just one study. This large sample greatly enhances the reliability of the conclusions drawn and thus can have a greater impact on our understanding of autism spectrum disorders.

This change does not add any risks to participants. Those participants who contributed full datasets (that is, structural and resting-state functional MRI as well as behavioral data) (n=30) will be informed of this new addition to the consent form and asked if they are willing to have their de-identified data contributed, which they will indicate by electronic signature on the revised consent form.

This change has no impact on the scientific integrity of the study.
The amendment was approved by local IRB on October 5, 2015 and submitted to HRPO who approved the amendment on December 5, 2015.

6. **PRODUCTS:** List any products resulting from the project during the reporting period. Examples of products include:

- **Publications, conference papers, and presentations**

- **Books or other non-periodical, one-time publications.**

- **Other publications, conference papers, and presentations**

Sand, L. A. (2015). Neural Bases of Emotional Language Processing in Individuals with and without Autism. Unpublished Doctoral Dissertation, University of Maryland College Park. http://drum.lib.umd.edu/bitstream/handle/1903/17242/Sand_umd_0117E_16641.pdf?sequence=1

- **Website(s) or other Internet site(s)**

List the URL for any Internet site(s) that disseminates the results of the research activities. A short description of each site should be provided. It is not necessary to include the publications already specified above in this section.

The Autism Brain Imaging Data Exchange (ABIDE):
http://fcon_1000.projects.nitrc.org/indi/abide/

The ABIDE dataset is a database of structural MRI and resting-state functional MRI scans as well as behavioral measures collected from children and adults with autism spectrum disorders and typically developing controls that multiple sites across the US (and some international) contribute data to. The goal is for researchers to be able to aggregate across sites with a sample much larger than is possible with just one study. This large sample greatly enhances the reliability of the conclusions drawn and thus can have a greater impact on our understanding of autism spectrum disorders.

- **Other Products**

5. PARTICIPANTS & OTHER COLLABORATING ORGANIZATIONS

Provide the following information on participants:

- what individuals have worked on the project?
- has there been a change in the other active support of the PD/PI(s) or senior/key personnel since the last reporting period?
- what other organizations have been involved as partners?

What individuals have worked on the project?

Name:	Donald J. Bolger
Project Role:	Principal Investigator
Researcher Identifier (ORCID ID):	0000-0001-5114-8484
Nearest person month worked:	0.85 Academic, 3.0 summer
Contribution to Project:	Dr. Bolger oversaw the execution of the research protocol and monitored both recruitment and research protocols.
Name:	Elizabeth Redcay
Project Role:	Co-Investigator
Researcher Identifier (ORCID ID):	0000-0002-1568-3102
Nearest person month worked:	0.85 Academic, 1.0 summer
Contribution to Project:	Dr. Redcay was active in the planning of the project and has provided support to Dr. Sand in the running of participants.
Name:	Lesley Sand
Project Role:	Graduate Student/Postdoctoral Researcher
Researcher Identifier (ORCID ID):	0000-0002-0893-4081
Nearest person month worked:	9.0 Academic, 3.0 summer
Contribution to Project:	Dr. Sand was largely responsible for recruitment of participants and execution of the research protocol.
Name:	Tom Zeffiro
Project Role:	Consultant
Researcher Identifier (ORCID ID):	0000-0002-0893-4081
Nearest person month worked:	0.25 Calender (unpaid)
Contribution to Project:	Dr. Zeffiro has been an unpaid consultant who has provided previous training to Dr. Sand on functional brain imaging analysis and continues to advise on data analysis and imaging protocols.
Name:	Laura Casey
Project Role:	Undergraduate Researcher
Researcher Identifier (ORCID ID):	
Nearest person month worked:	0.25 Calender (unpaid)
Contribution to Project:	Ms. Casey worked alongside Dr. Sand as an undergraduate research to help analyze MRI data.

Has there been a change in the active other support of the PD/PI(s) or senior/key personnel since the last reporting period?

There is no change in overall effort by the PIs. Dr. Redcay's R01 proposal was funded in 2015 (details below). However, there is no overlap in effort or project goals.

NICHD R01
Hippocampal-memory network development and episodic memory in early childhood
Role: co-I; time committed 1.35 academic months/year for 5 years
Direct costs: $1,835,112

Overlap: None

Project Description: These studies will examine structural and functional development of hippocampal-memory network in early childhood and its relation to episodic memory abilities.

What other organizations were involved as partners?

Nothing to Report

6. SPECIAL REPORTING REQUIREMENTS: None

7. **APPENDICES:** Attach all appendices that contain information that supplements, clarifies or supports the text. Examples include original copies of journal articles, reprints of manuscripts and abstracts, a curriculum vitae, patent applications, study questionnaires, and surveys, etc.

ABSTRACT

Title of Document: NEURAL BASES OF EMOTIONAL LANGUAGE PROCESSING IN INDIVIDUALS WITH AND WITHOUT AUTISM

Lesley Ann Sand, Doctor of Philosophy, 2015

Directed By: Associate Professor Donald J. Bolger
Department of Human Development and Quantitative Methodology

A fundamental aspect of successful social interactions is the ability to accurately infer others' verbal communication, often including information related to the speaker's feelings. Autism spectrum disorder is characterized by language and social-affective impairments, and also aberrant functional neural responses to socially-relevant stimuli. The main objective of the current research was to examine the behavioral and neural effects of making affective inferences from language lacking overt prosody or explicit emotional words in individuals with and without autism. In neurotypical individuals, the current data are consistent with previous studies showing that verbal emotional stimuli enhances activation of brain regions generally responsive to discourse, and also "social-affective" brain regions, specifically medial/orbital frontal regions, bilateral middle temporal areas, temporal parietal junction/superior temporal gyri and pCC/PC. Moreover, these regions

respond differentially to positive and negative valence, most clearly in the medial frontal area. Further, results suggest that mentalizing alone does not account for the differences between emotional and neutral stories, as all of our stories required similar inferencing of the feelings of the protagonist. In autism, there is general agreement that the neurodevelopmental disorder is marked by impairments in pragmatic language understandings, emotional processes, and the ability to "mentalize," others' thoughts, intentions and beliefs. However, findings are mixed regarding the precise nature of emotional language understandings. Results of the present study suggest that autistic individuals are able to make language-based emotional inferences, and that like neurotypical controls, social-affective brain regions show task-related facilitation effects for emotional compared to neutral valence. However, the neural activations in the autism group were generally greater than controls, especially in response to emotion. Additionally, results showed greater difficulty with incongruent judgments in participants with autism. Together, these findings represent a first step toward revealing social-affective abilities in the language context in autism, despite irregular brain response. Such understandings are critical to generating effective intervention strategies and therapeutic practices for autistic individuals and their families. For remediation to be most beneficial, one must understand and utilize areas of skill, and leverage those to positively impact deficits.

NEURAL BASES OF EMOTIONAL LANGUAGE PROCESSING IN INDIVIDUALS WITH AND WITHOUT AUTISM

By

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Dedication

I dedicate this work to my husband Ole Christian, whose never-ending enthusiasm for my work has motivated and encouraged me. To Nicolai, Christian, Haakon and Lillian, thank you for tolerating a distracted mother and fewer home-cooked meals for a few years.

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Chapter 1 - Introduction

Autism is a neurodevelopmental disorder marked most notably by a profound and life-long social disability affecting one's ability to establish and maintain reciprocal relationships and further defined by language and communication impairments, behaviors that are repetitive or ritualistic, and affective abnormalities. (American Psychiatric Association, 2013; Klin, Jones, Schultz, Volkmar, & Cohen, 2002; Volkmar, Lord, Bailey, Schultz, & Klin, 2004; Westphal & Volkmar, 2008). Due to the integral nature of social functioning for humans, this core deficit is highly detrimental as it concerns the ability to form and maintain relationships (Baron-Cohen, 1988; Baron-Cohen, Tager-flusberg, & Cohen, 1994; Landa, Holman, & Garrett-Mayer, 2007) which can negatively impact one's overall well-being and mortality (Achat et al., 1998; Berkman & Syme, 1979; Pearlin, 1985). Autistic adolescents[1] with autism report frequent feelings of loneliness, depression, dissatisfaction with the quality of their friendships, lower quality of life (QOL) ratings and higher rates of depression than their typically developing peers (Bauminger & Kasari, 2000; Bauminger et al., 2008; Begeer, Koot, Rieffe, Meerumterwogt, & Stegge, 2008; Hill, Berthoz, & Frith, 2004; Ikeda, Hinckson, & Krageloh, 2014; Kamp-Becker, Schröder, Remschmidt, Bachmann, & Schroder, 2010; Mayes, Calhoun, Murray, Ahuja, & Smith, 2011), and they are 28 times more likely to have suicide ideation or attempts than typical children (Mayes, Gorman, Hillwig-Garcia, & Syed, 2013). Similarly, autistic adults express lower QOL ratings,

[1] The terminology *autistic individuals* will be used to reflect preferred terminology of individuals with ASDs (Pellicano, Ne'eman, & Stears, 2011).

dissatisfaction in the quantity and quality of their social relationships, and also a desire for more meaningful social-emotional interactions (Grandin & Scariano, 1986; Grandin, 2009; Howlin, Mawhood, & Rutter, 2000; Khanna, Jariwala-Parikh, West-Strum, & Mahabaleshwarkar, 2014; Mazurek, 2013). These findings contradict Leo Kanner's initial belief that children with autism *preferred* solitude over the company of people: "so long as they left the child alone, [people] figured in about the same manner as did the desk, the bookshelf, or the filing cabinet" (Kanner, 1943, p. 246). The pervasive social impairments in autism also affects family members and loved ones; research suggests that parenting an autistic child is more stressful than raising one who is typically developing or one with Down syndrome (Baghdadli, Pry, Michelon, & Rattaz, 2014; Donovan, 1988; Morgan, 1988). The struggle to form a natural bond contributes to the stress; compared to typical children, autistic children are less likely to smile in response to their mother's smiles (Dawson, Hill, Spencer, Galpert, & Watson, 1990), attend to their mother's face (Joseph & Tager-Flusberg, 1997), orient to social stimuli (Dawson, Meltzoff, Osterling, Rinaldi, & Brown, 1998; Geraldine Dawson et al., 2004), and share positive affect in social contexts (Kasari, Sigman, Mundy, & Yirmiya, 1990).

In summary, among the triad of deficits that define autism, the social impairments are putatively the most serious concern for individuals with autism and also for their families. It is therefore not surprising that a longstanding goal of the research in autism has been to describe the systems involved in the hallmark social impairment, and to this end several theoretical frameworks have been proffered.

Theoretical approaches to autism

According to one theoretical model, “weak central coherence” (WCC), difficulties in understanding emotions in language are due to a more general deficit in formulating global inferences (Happé & Frith, 2006). This model was first proposed to explain the unique profile of superior performance in some areas requiring “local” processing, for example in visual discrimination tasks (O’Riordan & Plaisted, 2001; Plaisted, Riordan, & Baron-Cohen, 1998) along with impairments with more abstract tasks like arranging sentences in coherent order (Jolliffe & Baron-Cohen, 2000). Recently, it has been refined to predict reduced integration of global information (Happé & Booth, 2008). This is consistent with behavioral evidence suggesting autistic individuals are able to decode at the word level, but experience greater difficulties as text increases in complexity and requires more integration with other cognitive domains (Tager-flusberg, Paul, & Lord, 2005), as even high-functioning autistic individuals have difficulty with inferential language (Dennis, Lazenby, & Lockyer, 2001) and in disambiguating meaning from sentence context (López & Leekam, 2003). As such, this model is useful in explaining difficulties that autistic individuals may have with processing the “whole picture” of a social situation, and more specifically with making inferences from language per se.

A second theory—impairment of complex processing—proposes that multiple primary cognitive deficits are responsible for the unique behavioral profile observed in autism (Minshew & Goldstein, 1998). Accordingly, this model predicts that autistic individuals have relative strengths in the areas of attention, sensory perception, simple memory, simple language, rule-learning, and visuospatial areas; while deficits

occur in concept formation, complex language and complex memory. More recently, this theoretical model has been refined to predict that autism is predominantly a disorder of neural connectivity, particularly intrahemispheric connectivity (Minshew & Williams, 2007). This is compelling, and provides a common thread between these theories in that each is explained by the absence of a "central executive," or a failure of the top-down control processes to modulate bottom-up information processes. Neuroimaging studies showing reduced connectivity provide evidence of this abnormality. In addition to examples provided above (in emotion- and language tasks), this neural profile is also shown in executive functions (Just, Keller, Malave, Kana, & Varma, 2012) visual processing tasks (Behrmann, Thomas, & Humphreys, 2006; Vandenbroucke, Scholte, van Engeland, Lamme, & Kemner, 2008) working memory tasks (Koshino et al., 2005) and during rest (Pierce & Redcay, 2008; Redcay & Courchesne, 2008).

A third theoretical model suggests that social impairments in autism are due to "mentalizing" or "theory of mind" (ToM) deficits (Frith & Frith, 1999, 2003; Frith, 2001). The concept of mentalizing refers to the ability to understand, describe and explain others' behaviors in terms of their mental processes (beliefs, intents, desires, etc.). As emotions are at least partially a mental state, it is easy to see how impairments in mentalizing would impact one's social understandings. Proponents of this theory postulate that this is not a learned skill, or a product of logical inference, but instead rooted in a neurocognitive system comprised of a subgroup of the "social brain" network: medial prefrontal regions and bilateral posterior superior temporal sulci and anterior temporal poles (coined the 'ToM network') (Frith & Frith, 2003;

Gallagher & Frith, 2003; Saxe & Kanwisher, 2003; Saxe & Powell, 2006). Impaired connectivity within this network (Baron-Cohen et al., 1999; Castelli, 2005; Kana, Keller, Cherkassky, Minshew, & Just, 2009; Piggot et al., 2004) is believed to underlie the social deficits seen in autistic individuals because they are unable to conceive mental states (like others' beliefs), and cannot predict or anticipate others' behaviors or actions. By extension, the ToM network is associated with the communicative deficits in autism as language development is closely linked to joint attention and understanding the communicative intent of others' (Baron-Cohen, 1997; Tomasello & Farrar, 1986). However, an important distinction is made between mental states (associated with verbs like *want, know, pretend*) and emotional states (associated with adjectives like *disappointed, sad, ecstatic*); as such the notion of "mind blindness" does not directly account for impaired emotional processing in autism, but considers it a secondary deficit, dissociable from mentalizing. This distinction has also been made at the neurophysiological level, as emotional stimuli are associated with brain activations in the "emotional brain network" specifically the amygdala, the orbitofrontal cortex and the anterior cingulate cortex. In neurotypical adults, for example, the medial orbitofrontal lobe is preferentially involved with emotional processing (Beauregard et al., 1997; Hynes, Baird, & Grafton, 2006; Maratos, Dolan, Morris, Henson, & Rugg, 2001), and in autism, response differences have been shown in emotion-related brain regions (e.g., the amygdala and ventral prefrontal cortex) during processing of emotional facial expressions (Ashwin, Baron-Cohen, Wheelwright, O'Riordan, & Bullmore, 2007; Baron-Cohen et al., 1999; Piggot et al., 2004; Wang, Dapretto, Hariri, Sigman, & Bookheimer, 2004; Weng et

al., 2011) or during processing of emotional prosody (Tesink et al., 2009; Wang, Lee, Sigman, & Dapretto, 2006). In summary, the ToM proposal may not fully characterize the nature of the putative relationship between language- and emotional processing deficits and social functioning in autism, but provides a framework for understanding how impairments within ToM regions and the emotional network may be underlying factors.

In summary, there is considerable evidence suggesting that there is a neural basis for the social impairments that characterize autism, but disentangling the factors associated with this social dysfunction is challenging. The current research study focuses on two domains critical to social functioning: emotions and language processing. The fact that both figure prominently among the diagnostic criteria begs the question: “Are language- and emotional processing deficits related to the observed social impairments in individuals with autism, and if so, what is the nature of this relationship?” The first goal of this dissertation is to summarize the empirical findings related to affective language processing in autism.

Behaviorally, many recent studies suggest autistic individuals can adequately process emotional words in the context of language. However, processing of emotional words may rely on a purely abstract semantic index of meaning rather than evoking an emotional response from the linguistic information. Because this is often difficult to tease apart in behavioral paradigms, neuroimaging methods are ideal to determine whether the same emotional systems are activated for autistic individuals relative to neurotypical individuals when inferring emotions from language context.

Thus the second goal of this research is to conduct a neuroimaging study that may provide insight into the differential processing of emotional language for autistic individuals relative to typically developing individuals. The main hypothesis is that neural activations in language and emotional regions will be atypical in autistic individuals compared to neurotypical controls.

The following chapters adhere to the aforementioned goals. Chapter 2 provides an overview of how emotional understandings develop in typical individuals, and also describes the interdependence between communication and emotional competence; both are presented as they relate to social abilities and interactions. This is followed by a summary of the empirical findings related specifically to affective language processing in autism. Chapter 3 reports the results of Study 1, designed to investigate the neural processes of affective language processing in neurotypical individuals[2]. This study provided the background for extending the paradigm to individuals with autism, details of which are presented in Chapter 4.

[2] This chapter is adapted from a manuscript in preparation by: Sand, L., Redcay, E., Zeffiro, T. and Bolger, D.J.

Chapter 2 - Literature review

While defined by a triad of deficits, autism is most notably recognized by impaired social abilities (Klin et al., 2002), which can lead to significant difficulties in personal relationships and quality of life (Achat et al., 1998; Berkman & Syme, 1979; Pearlin, 1985). This review will address two domains essential to social interactions: emotion- and language processing. Due to the complex nature of both areas, it is useful to view these findings in concert with related skills and processes (Figure 1). Therefore, I first provide a brief overview of how emotional understandings develop in typical individuals, and also describe the interdependence between communication and emotional competence. Both are presented in light of their relationship to social abilities and interactions. Next, I summarize the empirical findings related specifically to the ability of autistic individuals to make affective inferences from language.

Background and overview

Social interactions are complex; necessarily involving the experience of feelings, as well as the ability to send and receive emotional messages (Adolphs, 2002, 2003; Denham, Bassett, & Wyatt, 2007; Halberstadt, Denham, & Dunsmore, 2001; Salovey & Grewal, 2005). Throughout life most emotions are anchored in interactions with others, and the exchange of emotions defines interpersonal relationships. Similarly, social behaviors are regulated by an individual's ability to experience feelings and both send and receive affective messages (Adolphs, 2003; Halberstadt et al., 2001). So important are emotional understandings to

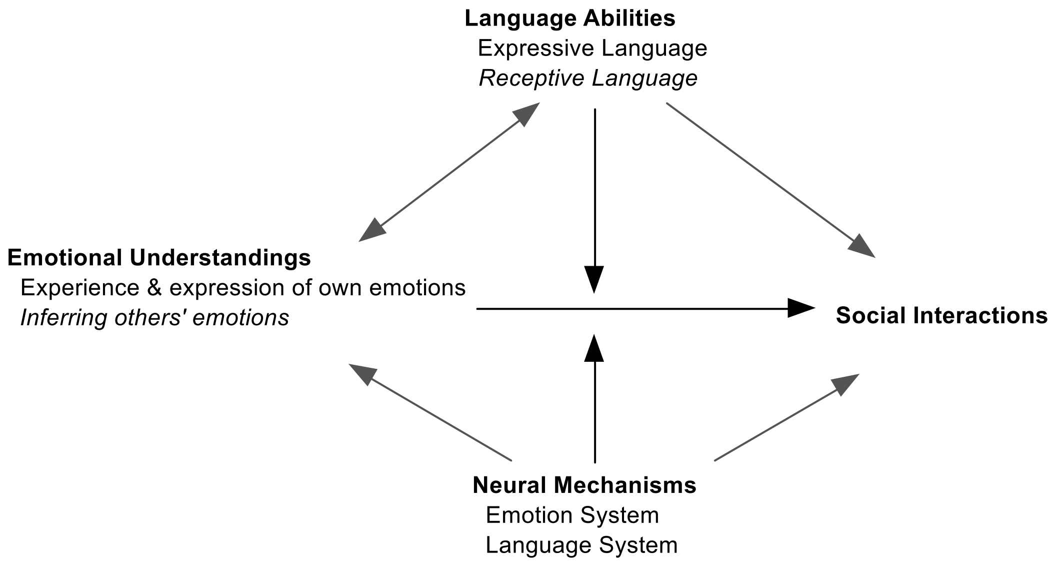

Figure. 1. Summary of mechanisms related to social interactions. The main focus of this research is the ability of individuals with ASD to infer others' emotions; this implies receptive language skills. However, emotional understandings include both one's own physical feelings and expressions of emotion as well as the ability to extend these understandings to others', and language skills include both expressive and receptive capacities. Neural systems related to both language- and emotion processes are well-defined, and impaired in autism.

social interactions that the term "emotional intelligence" was coined to describe the ability to perceive, use, understand, and manage emotions and to use this information to guide one's thinking and actions (Mayer, Salovey, & Caruso, 2004; Salovey & Mayer, 1989; Salovey & Grewal, 2005), thus tying these skills to social relationships. In fact, one's emotional intelligence predicts success in both personal and professional relationships (Brackett, Warner, & Bosco, 2005; Lopes et al., 2004; Lopes, Grewal, Kadis, Gall, & Salovey, 2006). Like adults, children's emotional understandings enhance their ability to relate to others and also impact their reputations. Youngsters scoring highest on emotional understandings tests are more popular among peers and display more socially acceptable behaviors (Cassidy, Parke, Butkovsky, & Braungart, 1992; Denham, McKinley, Couchoud, & Holt, 1990), and

elementary school children able to quickly and accurately infer emotions from facial expressions are more popular with their classmates (Edwards, Manstead, & MacDonald, 1984).

Like emotional understandings, fluent communication skills are integral to successful relationships and social interactions (Snow, 1999; Tomasello & Farrar, 1986; Tomasello, 2009). This relationship too, is symbiotic: children's language development is linked to their social environment (Hoff, 2006) and social understandings (Snow, Pan, Imbens-Bailey, & Herman, 1996; Snow, 1999), and emotional systems contribute to language comprehension (Havas, Glenberg, & Rinck, 2007). In typical children, the interplay between these systems is evident in their development and appears to emerge effortlessly as they interact with others.

Infants' early communication is founded upon emotional impulses, and their emotions are almost exclusively associated with their caretakers (Dunn, 2003). They quickly learn to comprehend the others' emotions by associating a verbal label or visual cue (e.g., facial expression) with their own emotion (Brown & Dunn, 1992; Edwards et al., 1984; Pons, Harris, & Rosnay, 2004). Later, processing these symbolic cues requires integrating the present situation to memories of a remote event. While both language capacities and cognitive factors are necessary for acquiring symbolic representation of feelings (e.g., emotional labels), intrapersonal perceptions of the symbol influence one's interpretation of that stimulus (Dolan, 2002). Thus, differentiating between emotions is suggested to be contingent upon a child's understanding of cause and effect, that is, one cannot understand a feeling

before experiencing it first-hand, and further being able to compare one's own behavior to a standard (Yarrow, 1979).

It follows that both emotional impairments (Begeer et al., 2008; Gaigg, 2012; Nuske, Vivanti, & Dissanayake, 2013; Uljarevic & Hamilton, 2013), and language deficits characteristic of autism may be related to their social deficits. Indeed, language is a primary mechanism by which emotional states are communicated, specifically the ability to infer emotions implied from language context is a critical aspect of fluent communication in everyday social interactions. The question remains whether the locus of the emotional impairments is in: a) the perception of nonverbal cues of emotion, b) the physiological response to emotion, or c) processes related to encoding emotional information and/or d) how these factors contribute to the difficulties with understanding others' emotions via language.

Nonverbal emotion perception in autism

In autism, many studies investigating emotional perception abilities have used facial stimuli, possibly due to the importance of facial expressions in social competence (Calder & Young, 2005). Results from behavioral studies are mixed, with some studies suggesting impaired perception of emotion from faces (Adolphs, Sears, & Piven, 2001; Bormann-Kischkel, Vilsmeier, & Baude, 1995; Grossman & Tager-Flusberg, 2008; Hubl et al., 2003), while others suggest intact abilities (Gross, 2004; Ozonoff, Pennington, & Rogers, 1990). A recent review (Harms, Martin, & Wallace, 2010) sheds light on these behavioral findings, concluding that autistic individuals infer emotion from facial expressions differently from neurotypical controls. Likewise, behavioral studies using nonverbal cues other than whole, static faces

however appear to converge on a profile of behavioral impairment. Examples include difficulties in recognizing complex emotions and mental states from pictures of the eyes (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001) through inflections of the voice (Golan, Baron-Cohen, Hill, & Rutherford, 2007; Mazefsky & Oswald, 2007; Rutherford, Baron-Cohen, & Wheelwright, 2002), and in films depicting social situations (Heavey, Phillips, Baron-Cohen, & Rutter, 2000).

Other nonverbal cues of emotion fail to elicit typical responses in autistic individuals as well, as autistic children pay less attention and show reduced affect toward an experimenter who pretends to hurt herself (Corona, Dissanayake, Arbelle, Wellington, & Sigman, 1998; Sigman, Kasari, Kwon, & Yirmiya, 1992) and do not display normal neurophysiological responses to others' pain (Minio-Paluello, Baron-Cohen, Avenanti, Walsh, & Aglioti, 2009). Neuroimaging studies also reveal differences in cortical and subcortical responses between autistic and typically developing participants in emotion-related brain regions (e.g., the amygdala and ventral prefrontal cortex) during processing of emotional facial expressions (Ashwin et al., 2007; Baron-Cohen et al., 1999; Critchley et al., 2000; Dapretto et al., 2005; Gaigg, 2012; Harms, Martin, & Wallace, 2010; Piggot et al., 2004; Wang et al., 2004; Weng et al., 2011). A related study by Hubert, Wicker, Monfardini, & Ceruelle (2009) also supports the notion of impaired neural processing; they showed that, unlike the control group, autistic individuals failed to exhibit changes in skin conductance responses (SCRs) to emotional expressions (but see Corden, Chilvers, & Skuse, 2008), and researchers have shown the importance of the amygdala in modulation of autonomic responses (Lang, Tuovinen, & Valleala, 1964). Studies of

encoding or retrieval of emotional information from memory can give insight into difficulties with emotion processing in autism.

Encoding emotional information

A plethora of studies have shown that emotional stimuli are more salient than neutral, and that humans remember emotional stimuli more effectively than neutral (Hamann, 2001; Reisberg & Hertel, 2004). This is true for experiences (Adolphs, Cahill, Schul, & Babinsky, 1997; Cahill, Babinsky, Markowitsch, & McGaugh, 1995; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000), pictures (Cahill et al., 1996; Hamann, Ely, Grafton, & Kilts, 1999; Harris & Pashler, 2005; Talmi, Schimmack, Paterson, & Moscovitch, 2007), as well as for language (Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003; Kensinger, 2007; LaBar & Cabeza, 2006; Maratos et al., 2001). Additionally, emotional words evoke faster (Kousta, Vinson, & Vigliocco, 2009) and more accurate (Eviatar & Zaidel, 1991) responses than do neutral. While the influence of emotion on memory is well established in typically developing individuals, in autism findings suggest processing deficits specific to emotionally laden stimuli. For example, autistic adults failed to show an advantage for emotional- relative to neutral (Rosch, 1999) pictures (Deruelle, Hubert, Santos, & Wicker, 2008), words (Kennedy, Redcay, & Courchesne, 2006) and sentences (Beversdorf et al., 1998), but have shown intact short-term recall of emotionally salient (South et al., 2008) and taboo words (Gaigg & Bowler, 2008). In the latter study, the authors noted that autistic participants also remembered more (neutral) semantically-related words, and suggest that the enhanced recall in both instances could be due to semantic category effects (Rosch, 1999). Another notable finding was that, unlike the controls,

autistic individuals failed to show enhanced memory for either the emotional or semantically-related words either one hour or one day later, suggesting atypical encoding (interestingly, the autism group forgot the arousing- but *not* the neutral words). Another study designed to tease apart the influence of valence and semantic category on memory (Gaigg & Bowler, 2009a) used a memory illusion paradigm, as evidence suggests that individuals with autism are susceptible to illusory memories for semantically related target lures (Beversdorf et al., 2000; Bowler, Gardiner, Grice, & Saavalainen, 2000; Hillier, Campbell, Keillor, Phillips, & Beversdorf, 2007). While the control group showed less susceptibility to illusory memories for emotionally charged compared to the neutral words, the adults with autism did not show this effect. These findings, when taken together with results from their previous study (Gaigg & Bowler, 2008) as well as those from semantically related illusory memories in autism, suggest that encoding of affective words is generally indistinct from neutral words in autism. This leads me to my primary question, that is, how is emotional or affective language processed in individuals with ASD?

Affective Language Processing in Autism

Language competence is complex, including a) expressive and receptive skills, b) verbal and non-verbal cues (pragmatic language), and c) explicit ("*He felt sad.*") or implied ("*Her bike was stolen.*") messages. The latter may well present the greatest challenge to individuals with autism due to their unique language profile. In autism, lower level processing skills (phonology and syntax), are generally intact, while the "higher level" functions, including semantic (Harris et al., 2006) and pragmatic skills are characteristically deficient in autism (Groen, Zwiers, van der

Gaag, & Buitelaar, 2008; Loukusa & Moilanen, 2009; Rapin & Dunn, 2003; Tesink et al., 2009). Pragmatics is the linguistic domain concerned with the appropriate use of language in social contexts, and incorporates social, emotional and communicative behaviors (Adams, Baxendale, Lloyd, & Aldred, 2005). As such, pragmatics forms a critical intersection for language competencies and social interactions. Thus, even though many individuals with autism have some language capacities, rather than enhancing social exchanges and interpersonal relationships, evidence suggests that language weaknesses in autism may contribute to deficiencies in the social realm (Baron-Cohen, 1988; Kuhl, Coffey-Corina, Padden, & Dawson, 2005; Mundy, 2003). This is shown through weaknesses in identification of topic and making a relevant response (Adams, 2002; Tager-Flusberg & Anderson, 1991), maintaining a topic (Baltaxe & D'Angiola, 1992; Baltaxe, 1977), and gauging the quantity and quality of an utterance (Volden, 2002). **A**utistic individuals also show marked difficulties in taking account of the listener's perspective, and instead "lecture" about their own interests (Baltaxe, 1977; Fine, Bartolucci, Szatmari, & Ginsberg, 1994).

Weaknesses in understanding pragmatic language also reflect fundamental problems in knowing that one must infer the *intended* meaning of a message versus the literal content (Happé, 1993). In addition to being overly literal, (Attwood, Frith, & Hermelin, 1988; Attwood, 2006), autistic individuals also show weak inferencing skills (Ozonoff & Miller, 1996; Rumsey & Hamburger, 1990) difficulty understanding humorous material and jokes (Baron-Cohen, 1997; Emerich, Creaghead, Grether, Murray, & Grasha, 2003; Ozonoff & Miller, 1996; Samson &

Hegenloh, 2010), and interpreting figurative speech like lies, sarcasm, irony and metaphor (Happé, 1993; Tager-Flusberg, 1999).

Language competence is also an integral part of successful social-emotional processes in typical individuals (Havas et al., 2007; Tomasello, 2009), strongly suggesting that the hallmark pragmatic language deficits characterizing autism contribute significantly to deficiencies in the social realm (Baron-Cohen, 1988; Kuhl et al., 2005). The degree of social impairment in children with autism is in fact correlated positively with their language (dis)ability (Dawson et al., 2004; Tager-flusberg et al., 2005). Despite this, relatively few studies have systematically explored the ability of individuals with autism to understand emotions through the language context. Specifically, the ability to: a) identify and describe one’s own emotions, and b) understand the emotions of others via language.

Identifying and describing one’s own emotions

The acquisition of emotional language incorporates a myriad of facilities, including social development, cognitive abilities, and variables like linguistic abilities, age, and cognitive maturity (Van Lanker, Cornelius, & Needleman, 1991), suggesting that even though a child may have experienced an emotion, he may not yet be able to apply to appropriate lexical term (Lewis & Michalson, 1983). According to Wellman, and colleagues (1995), children as young as two years of age talk about both positive and negative emotions in themselves and others and frequently attribute emotions to dolls and pretend characters. Between 3 and 4, children recognize and label emotions based on expressive (facial) cues, and appreciate how external causes impact the emotions of other children (like receiving a gift) and by 5 or 6 they

understand that people may feel different emotions in the same situation depending on their desires and/or beliefs. By eight, children begin to appreciate “mixed emotions” and ambivalence, and also understand the emotional consequences of their actions (positive feelings follow praise-worthy actions, negative feelings are associated with shameful actions). By the age of ten, children’s abilities to decode emotions are generally adult-like (Custrini & Feldman, 1989; Pons et al., 2004), and characterized by a sophisticated reliance on situational cues to infer others’ emotional states (Camras, 1986) underscoring the complex interrelatedness of social cues—both verbal and nonverbal—with language and feelings. Not surprisingly, an important predictor of a child’s acquisition of emotional understandings is his or her rearing environment and use of language.

Two year olds’ talk about feelings correlates positively with the quality and quantity of references to emotional states made by their mothers and siblings six months earlier (Dunn, Bretherton, & Munn, 1987), and mother’s use of mental state language, not necessarily directed at the child, supports their children’s acquisition of internal state as well as their ability to correctly attribute emotions to story protagonists (Booth, Hall, Robison, & Kim, 1997; Pons et al., 2004). Frequent discourse about feelings in the family unit also enhances emotional understandings in children, as expressed both in their ability to identify emotions in pretend characters at three years of age and in more sophisticated affective understandings three years later (Brown & Dunn, 1992; Dunn et al., 1991). In these ways, language serves to enhance children’s emotional competence, which in turn effectively enriches their social capacities.

In summary, for typically developing individuals,emotional processes are contingent upon using and understanding emotional language, and affective verbal expressions carry complex information from several sources, including introspective information, observations relevant to one's own behavior, and semantic information. Adding to this complexity, emotions can be categorized differently, for example "simple" or "non-social" emotions (e.g., *fear* and *happiness*) are often juxtaposed to "complex," "abstract" or "social" emotions (e.g., *pride* and *embarrassment*) (Levenson, 1999). In the autism research, some studies suggest that the differentiating factor between ability and impairment lies in this qualitative distinction, whereas others report adequate abilities in both areas. In general, task demands appear to be a factor.

Identifying emotional words

The most rudimentary tasks regarding emotional language processing are at the single word level. For example, autistic children were able to accurately match simple emotional adjectives, e.g., *hurt* and *sad* (Van Lanker et al., 1991), to a line drawing, but autistic adults showed impairments when matching complex emotional words, e.g., *disagreement* and *embracing* to line drawings (Hobson & Lee, 1989). These divergent findings could be due to the level of difficulty of the words (see Appendix A for stimuli from both studies) and also because Van Lanker et al. (1991) included words that could describe a physical state (e.g., *lazy*, *sleepy*) in their emotional adjectives, and such words can be considered less abstract that strictly emotional state words. During another matching task, like typical controls subjects autistic children were able to match simple emotional labels (*happy*, *sad*, *angry*,

scared) to corresponding faces (Fink, de Rosnay, Wierda, Koot, & Begeer, 2014; Grossman, Klin, Carter, & Volkmar, 2000) but showed significant difficulty identifying simple emotions when a face was paired with a mismatched label, e.g., a happy face with the word *afraid* (Grossman, Klin, Carter, & Volkmar, 2000).

Interestingly, Fink et al. (2014) found that the autistic children had significantly *higher* accuracy rates during the pre-test phase of word-word matching, but when controlling for pre-test accuracy, their accuracy performance in the word-face test was significantly *lower* than controls. Other studies also highlight the finely-tuned distinction between ability and disability. Using an attentional blink (AB) paradigm with negative and neutral words, Corden et al. (2008) showed that autistic individuals performed equally well as controls in identifying the emotional words in general, but that controls demonstrated significantly greater accuracy at the shortest (120 ms) time lag. In a related AB study (Gaigg & Bowler, 2009b) using negatively valenced (profanity, taboo) words along with neutral words and male proper names, the emotional words failed to capture the attention of the ASD participants as readily as did the controls. Further, during a lexical decision task (word vs. nonword), like the control group individuals with ASD responded more quickly to emotional (both positive and negative) words than to neutral words, but their overall reaction times were significantly slower (Lartseva, Dijkstra, Kan, & Buitelaar, 2014). A final study revealed that autistic teens were significantly less able to identify one unpleasant word among three pleasant words compared to control participants (Han, Yoo, Kim, McMahon, & Renshaw, 2014).

Describing emotional states

More challenging tasks require verbal descriptions or responses regarding emotion, and here too results are mixed. For example, when asked to *explain* feelings of simple emotions like *happiness* or *sadness*, both autistic children and adults were able to provide contextually appropriate responses (Capps, Yirmiya, & Sigman, 1992; Jaedicke, 1994; Losh & Capps, 2006; Rieffe, Meerum Terwogt, & Kotronopoulou, 2007; Van Lanker et al., 1991; Yirmiya & Sigman, 1992), although their narrative descriptions differed from typical controls in terms of quality and content (fewer synonyms, fewer generalizations and examples, more concrete responses). However, deficits were revealed when autistic children were asked to describe complex emotions, e.g., *curious* and *surprised* (Losh & Capps, 2006) and also complex self-conscious emotions, e.g., *pride* and *embarrassment* (Capps et al., 1992; Losh & Capps, 2006; but see Yirmiya & Sigman, 1992). During more free-form conversations and narratives, most evidence suggests that autistic individuals use fewer emotional references. For example, autistic children showed "pragmatically problematic" responses to social-emotional- relative to neutral questions (Adams, Green, Gilchrist, & Cox, 2002), included less emotional information when retelling a story after a slide show compared to both controls and participants with Williams syndrome (Pearlman-Avnion & Eviatar, 2002), and used fewer emotional terms when dicussing memories (Brown, Morris, Nida, & Baker-Ward, 2012) and storybook characters (Siller, Swanson, Serlin, & Teachworth, 2014). In contrast, others have shown that autistic individuals are unimpaired in describing *both* social and non-social emotions, and providing examples of experiences of the same. For example, compared to age- and verbally-matched controls, autistic children were able to

describe past experiences of *pride* and *guilt* (Hobson, Chidambi, Lee, & Meyer, 2006), and replicating Losh and Capps (2006), Williams & Happé, (2010) failed to find differences between children with autism and matched controls in either definitions of emotional terms *or* in reflecting on an emotional experience. Similarly, Bang, Burns, & Nadig (2013) failed to show between-group differences in autistic childrens' production of emotional terms during conversations.

Other findings suggest anomalous *causes* of emotions, even though their responses were considered to be accurate. For example, autistic participants offered objects or material events as causes for feeling happy, sad, afraid, worried or angry (e.g., parties, living situations, or toys), while the majority of the comparison group made references to interpersonal or social causes (Jaedicke, 1994). Rieffe et al. (2007) corroborated these findings; 90% of their 10 year old subjects with autism gave a material reason for feeling happy ("when I am looking at my science book") while at least half of the comparison group provided social examples ("when I am with my friends"). Together, the findings related to identifying simple versus complex emotions in autistic individuals appear to be inconclusive, at least in the laboratory setting. However, both descriptions and causes of emotions in autism are more often noted as being abnormal or anomalous compared to typically developing individuals, which could reflect a) language deficits or b) aberrant encoding/processing of emotions.

Understanding others' emotion from language

The relatively sparse literature on situated social-emotional experiences with language uses sentences and short vignettes with implicit emotional content. These

studies reveal that individuals with autism are able to infer others' emotions—both simple and complex—from the language context. Autistic children successfully predicted a protagonist's emotion from stories designed to evoke a single emotion (Rieffe, Meerum Terwogt, & Stockmann, 2000) and also in stories depicting more than one emotion of the opposite- (*happiness/sadness*) or same valence (*anger/sadness*) (Rieffe et al., 2007). Additionally, autistic individuals successfully recognized social factors that would increase the potential for embarrassment—presence and type of audience or the act being witnessed by another person—and ably rated the level of embarrassment felt by the protagonist from short vignettes (Hillier & Allinson, 2002).

Real-time emotional processing in actual social situations requires fluid and simultaneous understanding of other's emotions inherent in their verbal and nonverbal cues. More challenging ecologically-valid paradigms attempt to use stimuli that presents information in multiple modalities, more closely associated with these experiences (Noller, 1985). As inferring emotion from multiple channels has been shown to be difficult for individuals with autism (Charbonneau et al., 2013; Hobson, 1986; Hobson, Ouston, & Lee, 1988; Hobson, 1988; Loveland et al., 1995; Woynaroski, Stevenson, & Wallace, 2013), efforts have been made by researchers to disentangle the contributing factors, be they verbal or nonverbal in nature. Here, too, however, contributions are few, and findings are mixed. Autistic adults were able to judge an actor's feelings from audiovisual clips where emotion was implied or explicit based on the verbal content of the script (explicit, implicit or neutral) and the emotional affect of the speaker (flat or animated expression delivered through both

facial expression and tone of voice) (Loveland et al., 1997), and like controls they exhibited greater difficulty in the mismatched conditions (explicit verbal content/flat affect and neutral verbal content/animated affect). Autistic children and adolescents also demonstrated competence in judging videotaped scenes from the Perception of Emotions Test (Egan et al., 1998). Each scene includes actors depicting an emotion (happy, angry, sad, or neutral) in a different modality (static face, dynamic face, prosody, verbal content or combined), and autistic participants performed as well as the typically developing children in the two tasks including verbal content: the audio recordings and the scenes using combined modalities. However, their performance on the other three tasks (static face, dynamic face and tone of voice) was impaired compared to the control subjects (Lindner & Rosen, 2006). Downs and Smith (2004) evaluated emotional understandings in autistic children using a battery of questions developed by Howlin, Baron-Cohen, & Hadwin, (1999). While the children with autism were significantly worse at identifying facial affect in photographs than the comparison groups, there were no differences between groups in any of the tasks involving verbal scenarios, suggesting that autistic children are equally able to infer other's emotions from verbal content paired with pictures as are typical children. Together, these findings suggest that autistic individuals are generally as able as ability-matched controls in inferring emotion from both implicitly- and explicitly stated verbal content, both independently and when combined with other modalities. Interestingly, like Grossman et al. (2000) and Fink et al. (2014), findings suggest that autistic individuals may have an overreliance on verbal information in the presence of nonverbal cues of emotion (Downs & Smith, 2004; Lindner & Rosén, 2006). The sum

of the evidence suggests that while the semantic content of words may be normally processed, emotional information may be abnormally encoded in individuals with autism. One's own emotional understandings subserve the ability to make inferences about others' emotional states, indeed this is at the heart of empathy. To make these inferences, however, one must quickly process both verbal and nonverbal cues, map them to one's own experiential store of emotional states, and apply this knowledge to another human actor. While the behavioral literature indicates that autistic individuals appear perform similarly to typically achieving peers when *comprehending* emotional language, the neuroimaging literature suggests that the processes underlying this process are quite different. Thus, the question is: in autistic individuals, how are verbal cues of emotion represented, or encoded within their own emotional systems, at the cortical and subcortical level?

Neural processing of emotional language

Although contributions are few, neuroimaging studies suggest differential processing of affective language in ASD as compared to typically developing controls. During complex text comprehension for example, participants with ASD failed to demonstrate differential cortical activations in response to any of the conditions (intentional-, emotional- or physical context), while the control group showed differential processing among inference types (Mason, Williams, Kana, Minshew, & Just, 2008). Further, autistic participants recruited both left and right hemisphere language areas (including the right middle- and superior temporal gyrus) to a larger extent than the control group in all conditions, suggesting a) they did not differentiate between the semantic representations of the language conditions, and b)

they engage putative semantic regions more heavily when comprehending discourse. (See Table 1 for general acronym definitions, and the Glossary for a complete list.) Functional connectivity was also aberrant in these participants with ASD: during the intentional passages, the autism group showed reduced connectivity between the ToM and language networks (left inferior frontal gyrus and left superior temporal gyrus). While behavioral results were not reported for this study, the authors reported that for individuals with autism, regional activation showed similar processing patterns regardless of task difficulty, and that this pattern reflected the brain areas activated in controls in the most difficult condition.

Table 1.

Acronyms for brain regions

X/Y	Z	Lobe/region	Gyrus/sulcus/cortex
a = anterior	S = superior	F = frontal	G = gyrus
p = posterior	M = middle	T = temporal	S = sulcus
l = left	I = inferior	P = parietal	C = cortex
m = medial		C = cingulate	
r = right		PF = prefrontal	
b = bilateral		TPJ = temporoparietal junction	

Differences in neural activations between autistic and control participants were also found during a task requiring congruency judgments using sentence context (emotional-, physical state- and concrete conditions). While there were no behavioral differences between groups, the emotional condition elicited activations within the fusiform gyri, right inferior parietal region and left superior temporal gyrus in the control group, while cortical activations in the autism group failed to reach significance (Catarino et al., 2011). Further, in an emotional counting Stroop task, negative (as compared to neutral) emotional words recruited a region within ventral

medial prefrontal cortex in neurotypical adults but no difference between conditions was seen in autistic adults (Kennedy et al., 2006). Finally, during an word identification task, emotion (positive and negative combined) words (compared to neutral) elicited significantly more activation in right fusiform gyrus and right middle temporal gyrus in autistic teens relative to neurotypical controls (Han et al., 2014).

Taken together, a pattern emerges of differential or abnormal integration of neural networks used for language and emotion processing in autism even in the face of equivalent behavioral competence. To our knowledge no one has investigated the combined behavioral profile and neural mechanisms specifically related to emotional inferencing abilities from language in autism. Such investigations are necessary to disentangle whether the presumed deficits in inferring emotions in others is due to difficulties in the evoking of emotion, making complex inferences in language, or an interaction of the two.

Discussion

The behavioral evidence suggests subtle deficits in emotional language processing in autistic individuals, especially during narrative production where they use fewer emotional terms and references (Adams et al., 2002; Brown et al., 2012; Pearlman-Avnion & Eviatar, 2002; Siller et al., 2014, but see Bang et al., 2013). In other areas, a profile of relative competence emerges from these empirical investigations. First, autistic individuals seem to be able to correctly identify and describe basic emotions/emotional words (Capps et al., 1992; Jaedicke, 1994; Kennedy et al., 2006; Lartseva et al., 2014; Losh & Capps, 2006; Rieffe et al., 2007; Van Lanker et al., 1991). In terms of more complex, or social emotions, findings are

inconclusive, with several studies suggesting impairments (Capps et al., 1992; Han et al., 2014; Hobson, Ouston, & Lee, 1989; Losh & Capps, 2006), others suggesting intact or at least adequate abilities (Hobson et al., 2006; Williams & Happé, 2010; Yirmiya & Sigman, 1992), and still others are mixed depending on the task (Corden et al., 2008; Fink et al., 2014). Furthermore, evidence suggests intact abilities when judging other's feelings from verbal description, and also in identifying contexts which would contribute feelings of embarrassment (Catarino et al., 2011; Downs & Smith, 2004; Hillier & Allinson, 2002; Loveland et al., 1997; Rieffe et al., 2000; Rieffe et al., 2007). These findings may add a complicating element to theories (Frith & Happé, 1994) and studies that have shown impairments in the ability to understand intentions in language (Jolliffe & Baron-Cohen, 2000). Additionally, when affective language is paired with other modalities, findings suggest difficulties assimilating several signals simultaneously as well as a preference for verbal information in the face of multiple cues (Downs & Smith, 2004; Fink et al., 2014; Grossman et al., 2000; Lindner & Rosén, 2006).

This summary of the literature (see Table 2) raises an important consideration: Even though emotional concepts are inherently abstract, they are associated with words, or labels, and these can be learned in a more systematic fashion, at least at the level of semantics. That is, the use of a verbal label may help make these relationships explicit. In comparison it is more difficult to assign a rule, or label, to a facial expression or gesture because these are more implicit and difficult to decode without the advantage of explicit references to the cause and content of the underlying emotion. Consider that the majority of studies use a discrete number of

simple words either as stimuli *or* as response choices (Appendix A); distilling the task to include a narrow range of possible words, or labels. I propose that abilities displayed at the behavioral level are due to the learned semantic meaning of these simple labels, but that the ability to engage or activate these emotional states or feelings from language is much more tenuous. That is, emotional labels are subject to abnormal encoding, or processing at the neural level in autistic individuals, because of the failure to systematically engage the emotional system. Studies examining memory for emotional words and sentences as well as neuroimaging results provide support for this theory. In the former, short-term abilities and long-term and illusory memory deficits suggest that emotional information is processed similarly to neutral information. The argument is that emotional information is remembered semantically or categorically, but not for affective content (Gaigg & Bowler, 2008; South et al., 2008). These studies raise the possibility that autistic individuals may rely more heavily on semantics in order to process affective language, at least as measured in these behavioral experiments. An overreliance on semantics might also account for abilities in other domains described above, for example immature or idiosyncratic descriptions of emotion (Capps et al., 1992; Losh & Capps, 2003; Van Lanker et al., 1991), short term memory abilities for simple emotional words or taboo words (Gaigg & Bowler, 2008; South et al., 2008 but see Kennedy et al., 2006), and impairments in matching abstract emotion words (which are unfamiliar, and thus not committed to memory) to pictures (Hobson & Lee, 1989). Functional neuroimaging provides a valuable tool to examine behavioral abilities in concert with brain activity, and as such may be uniquely helpful in shedding light on the neural mechanisms related to

affective language processing in autism. The following chapters describe two studies related to this goal. The first was a study of emotional language processing conducted with neurotypical individuals, and the second study extends the findings of the first study to individuals on the autism spectrum.

Table 2.

Summary of affective language competence in ASD

Author (year)	**Stimuli**	**Findings: ASD relative to NT**
	Processing one's own emotions	
Expression/Experience		
Hobson and Lee (1989)	Verbally presented complex words with emotional (e.g., surprise), social (e.g., embracing), or abstract (e.g., tranquil) content	*Impaired* for complex emotion
Van Lanker et al. (1991)	Verbally presented simple emotional adjectives (e.g., happy, sad) object nouns (e.g., table), and neutral adjectives (e.g., furry)	*Intact* for simple emotion *Anomalous* description
Capps et al. (1992)	Visually presented simple emotions (happy, sad) and complex (proud, embarrassed)	*Intact* for simple emotion; *Impaired* for complex emotion; *Anomalous* description
Yirmiya et al. (1992)	Visually presented simple (happy, sad, afraid, angry) and complex (proud) emotions	*Intact* for simple emotion; *Intact* for complex emotion
Jaedicke et al. (1994)	Verbally presented simple emotions (happy, sad, afraid, worried, angry)	*Intact* for simple emotion *Anomalous* description
Adams, et al. (2002)	Verbal questions regarding social-emotional- or neutral topics	*Anomalous* for social-emotional
Hobson et al. (2006)	Verbally presented self-conscious complex (proud, guilty) emotions	*Intact* for pride; *Adequate* for guilt; *Anomalous* description

Author (year)	Stimuli	Findings: ASD relative to NT
	Processing one's own emotions	
Expression/Experience		
Losh and Capps (2006)	Verbally presented simple (happy, sad, afraid, angry, disgusted), complex (curious, disappointed, surprised), self-conscious complex (proud, embarrassed, guilty, ashamed) emotions and non-emotions (tired, sick)	*Intact* for simple emotions; *Impaired* for complex & self-conscious emotions *Anomalous* description
Rieffe et al. (2007)	Verbally presented simple emotions (happy, sad, afraid, angry)	*Intact* for happy *Impaired* for negative emotions *Anomalous* description
Williams et al. (2010)	Verbally presented simple/non-social (happy, sad, scared, surprised, disgusted) and complex/social (proud, guilty, disappointed, embarrassed) emotions	*Intact* for simple and complex emotion
Brown et al. (2012)	Autobiographical memory interview	*Impaired* inclusion of emotional terms
Bang et al. (2013)	Free conversation with researcher	*Intact* inclusion of emotional terms
Memory		
Beversdorf et al. (1998)	Verbally presented sentences with emotional or neutral valence	*Impaired* ST memory
Kennedy et al. (2006)	Visually presented counting Stroop task using negative, neutral and number words	*Impaired* memory
South et al. (2008)	Visually presented words with emotional or neutral valence	*Intact* ST memory

Author (year)	Stimuli	Findings: ASD relative to NT
	Processing one's own emotions	
Memory		
Gaigg and Bowler (2008)	Visually presented emotionally valent (taboo, profanities and sexually explicit), semantically related (fruit) and unrelated neutral words	*Intact* ST memory; *Impaired* LT memory
Gaigg and Bowler (2009)	Visually presented orthographically related neutral words and emotionally valent target lures	*Impaired* illusory memories
	Understanding others' emotions	
Words and stories		
Grossman et al. (2000)	Emotional faces (happy, sad, angry, afraid, surprised) paired with matched- and mismatched label	*Intact* identification matched *Impaired* identification mismatched
Rieffe et al. (2000)	Verbally presented stories conveying typical and atypical emotions (happy, sad, angry, afraid)	*Intact* identification
Hillier and Allinson (2002)	Visually and verbally presented stories conveying varying degrees of complex emotion (embarrassment)	*Intact* identification
Pearlman-Avnion & Eviatar (2002)	Visually presented slide show with emotional elements, retell story	*Impaired* inclusion of emotional terms
Downs and Smith (2004)	Visually and verbally presented stories conveying simple emotion (happy, sad)	*Intact* identification

Author (year)	Stimuli	Findings: ASD relative to NT
	Understanding others' emotions	
Words and stories		
Kennedy et al. (2006)	Visually presented counting Stroop task using negative, neutral and number words	*Intact* identification
Rieffe et al. (2007)	Verbally presented stories conveying single- and multiple emotions (happy, sad, angry, afraid)	*Intact* for single emotions; *Adequate* for multiple emotions
Corden et al. (2008)	Visually presented negative and neutral words in attentional blink paradigm	*Intact* identification overall; *Impaired* identification at shorter (120ms) time lags
Gaigg & Bowler (2009b)	Visually presented negative and neutral words in attentional blink paradigm	*Impaired* identification
Catarino et al. (2011)	Visually presented sentences with emotional-, physical state- and concrete context	*Intact* congruency judgment
Fink et al. (2014)	Emotional faces (happy, sad, angry, afraid, surprised) paired with matched label	*Impaired* identification after accounting for pre-test accuracy scores
Han et al. (2014)	Visually presented pleasant and unpleasant words	*Impaired* identification
Lartseva et al. (2014)	Lexical decision (word-nonword), positive, negative, neutral words	*Intact* identification (shorter RT to emotion) *Impaired* overall RT
Siller et al. (2014)	Retelling a story from a picture book	*Impaired* inclusion of emotional terms

Author (year)	**Stimuli**	**Findings: ASD relative to NT**
	Understanding others' emotions	
Multimodal		
Loveland et al. (1997)	Videos conveying simple emotion (happy, sad, angry, surprised, neutral) verbally, nonverbally or both	*Intact* identification
Lindner and Rosen (2006)	Videos conveying simple emotion (happy, sad, angry, neutral) in different modalities	*Intact* for verbal content; *Impaired* for nonverbal contexts

Note. Only information relating to emotional language is included from these studies. Abbreviations: ASD, individuals with autism; LT, long-term, NT, neurotypical individuals; ST, short-term.

Chapter 3 – Emotional language processing in neurotypical individuals

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Abstract

A fundamental aspect of successful social interactions is the ability to quickly and accurately comprehend the implied meaning of others' verbal messages, an ability requiring that the listener draw inferences often related to how the speaker feels. The objective of this study was to examine the neural correlates of language processing specifically related to emotional messages that require inferencing using functional magnetic resonance imaging (fMRI). For example, hearing "*My bike was stolen*" suggests that the speaker is unhappy, or angry. Participants (*n* = 22) listened to short vignettes describing a protagonist's emotional state (positive, negative or neutral), then responded to a true or false decision. Changes in the Blood Oxygenated Level Dependent (BOLD) contrast were analyzed separately for the story and the response period. Consistent with previous studies, emotional conditions elicited areas of activation in medial and orbital frontal regions as well as bilateral middle temporal areas, temporal parietal junction/superior temporal gyri and precuneus/cingulate cortex, regions that have been associated with both the processing of affective stimuli as well as social cognition in general. Moreover, these regions responded differentially to stimuli with either positive or negative valence, especially in the medial prefrontal cortex (mPFC), where negative stories elicited more dorsal mPFC and the positive condition was consistent with ventral mPFC. We additionally found

that activity in regions typically associated with belief representation (mPFC, anterior temporal lobes, and temporal/parietal junction) was significantly greater for emotional stories compared to neutral, demonstrating a role of these regions in making inferences about others emotional states beyond simply belief representation. Finally, contrary to previous research on emotional inferencing, we did not find subcortical activity, in the amygdala and striatum, during the story phase. However, this subcortical activation was exhibited in the context of the true/false congruency judgment, including the putamen, caudate, insula and amygdala, suggesting that previous findings may be due to decision-making factors on emotion.

Introduction

The study of language comprehension or discourse processing has generally focused on the ability to extract meaning from language form (the spoken or written content) and connect it to our extant knowledge of the world and how it works (Barsalou, Santos, Simmons, & Wilson, 2008; Kintsch, 1998; Walter Kintsch & Dijk, 1978). This process entails drawing inferences about content that is not explicitly stated but is dependent on the schemas activated from prior knowledge and our ability to access them. One specific aspect of discourse that is often implied, but not stated explicitly, is the affective context of the actors in a story, or of conversational partners. When a listener of a story hears about a particular event (e.g., a house fire), they are often left to infer how the actors in the story feel. These types of bridging inferences are elaborations on the information directly presented and, from a psycholinguistic perspective, are not obligatory or necessary to maintain the coherence of a story (Graesser, Singer, & Trabasso, 1994). Moreover, inferences

involving human actors involve social processes of mentalizing or Theory of Mind (ToM), in which the listener may more readily construct a situation model representation of the discourse. In such cases, it is argued that the listener engages "a mental model of the situation" including the social-emotional processes that would be evoked by the actor(s) in the story (Wellman, Cross, & Watson, 2001). As such, the processes involved in drawing such inferences may go beyond the simple linguistic/semantic and perceptual systems engaged in building such a representation to include emotion and ToM. The fundamental research question posed here is whether neural systems engaged when inferring an actor's emotional state differ compared to physical states such as energetic or fatigued.

Overall, the majority of findings on narrative comprehension in general reveal activation of medial frontal and bilateral temporal and parietal regions (Ferstl & Neumann, 2008; Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mar, 2004, 2011; Prat, Mason, & Just, 2012). More specific investigations of the neurobiology of inferential processing have generally shown a consistent set of cortical regions which include: bilateral anterior temporal lobes (aSTS) extending to the superior temporal sulcus (STS), inferior frontal gyrus (IFG), medial prefrontal cortex (mPFC) and posterior cingulate cortex/precuneus (pCC/PC). This network is argued to be engaged when elaborating upon the linguistic information presented beyond processing syntax and maintaining coherence, such as elaborative, bridging, or causal inferences (Jung-Beeman, 2005; Jung-Beeman et al., 2004; Tyler & Marslen-Wilson, 2008; Virtue, Haberman, Clancy, Parrish, & Jung Beeman, 2006). Additionally, discourse involving human characters invokes ToM processes, or the ability to attribute mental

states (e.g., beliefs or desires) to others and use this information to explain or predict their actions, motivations, intentions, etc. (Ferstl & von Cramon, 2002; Mar & Oatley, 2008). Brain regions typically involved in story-based ToM processing include medial PFC, temporal poles, bilateral posterior superior temporal sulcus and the posterior cingulate (Frith & Frith, 2003; Gallagher & Frith, 2003; Saxe & Kanwisher, 2003; Saxe & Powell, 2006). While this network (which overlaps with the putative "default mode network"; Spreng & Grady, 2009) is generally associated with mentalizing, functional divisions arise depending on the type of mental state attribution. Specifically, bilateral TPJ respond more to stories requiring representation of a character's thoughts than their physical description or enduring personality traits (Heberlein & Saxe, 2005) or to physical pain of that character (Bruneau, Pluta, & Saxe, 2012). Midline structures (mPFC and pCC/PC), however, are associated both with judgments about the transient contents of one's mind (e.g., thoughts and beliefs) as well as enduring personality traits or physical characteristics of the self and other (Mitchell, Macrae, & Banaji, 2006; Moran, Lee, & Gabrieli, 2011). What is apparent is that there is overlap in the cognitive and neural mechanisms for narrative comprehension and mentalizing (Mar & Oatley, 2008; Mar, 2011) in general a topic that we will directly address momentarily.

During verbal communication, knowledge or understanding of the speaker's emotions are made both from explicit emotional statements (e.g., "*I hate my teacher*") as well as language that implies an emotion or an emotion may be inferred (e.g., "*I got a new bike for my birthday*"). However, the majority of investigations of emotional language have employed arousing or valent words in isolation, thus

eliminating the need for inferencing (see Citron, 2012 for review). Recent studies in this area suggest that processing single affective words engages brain areas known to be associated with emotion. For example, the amygdala is activated in response to both highly negative (Isenberg et al., 1999; Kensinger & Schacter, 2006; Maddock & Buonocore, 1997; Maddock, Garrett, & Buonocore, 2003; Maratos, Dolan, Morris, Henson, & Rugg, 2001; Nakic, Smith, Busis, Vythilingam, & Blair, 2006; Tabert, Borod, Tang, & Lange, 2001) as well as positive words (Briesemeister, Kuchinke, Jacobs, & Braun, 2014; Hamann & Mao, 2002; Harenski & Hamann, 2006; Kensinger & Schacter, 2006; Maddock et al., 2003). Additionally, both positive and negative words evoke activations in medial/orbital frontal regions and cingulate cortex (Beauregard et al., 1997; Maddock et al., 2003; Maratos et al., 2001). However, emotionally arousing words—especially in isolation—do not reflect every day social discourse. Instead, verbal interactions typically consist of narratives that frequently connote mild and/or mixed emotions, and often require the listener to *infer* the feeling of the speaker. For example, if a listener hears, "*Frank worked all night on his report, but his computer crashed and he lost his work*," it is immediately understood to involve negative emotions, e.g., distress or frustration.

Whereas the literature on mentalizing and emotion are quite robust, neuroimaging studies of affective semantics at the sentence and story level are less prevalent. One report showed that listening to short emotional sentences spoken by both actors and machines (lacking prosody) recruited two general networks: 1) bilateral IFG, bilateral anterior insula, pre-supplementary motor area (SMA) as well as subcortical areas (left thalamus and right caudate nucleus), and 2) medial superior

frontal gyrus and left posterior STS (Beaucousin et al., 2007). In another study, participants listened to longer emotional scenarios (~45 sec) with inconsistencies embedded in the stories. When the inconsistency concerned emotion, activations were revealed in ventromedial prefrontal cortex (vmPFC), dorsal precuneus and left amygdaloid complex (Ferstl, Rinck, & von Cramon, 2005). Most social interactions, however, are not characterized by lengthy monologues. An investigation (Ferstl & von Cramon, 2007) using very short visually-presented emotional scenarios showed that aSTS, but not vmPFC or amygdala, was sensitive to the emotional content of the scenario. The authors suggested that the lack of response in medial structures may have been due to shallower processing of the short stimuli.

The bulk of the literature on inferring emotional states of others has generally been in comparison with more cognitive constructs of mentalizing (e.g., false beliefs, strategic thinking, or intentions etc.) to support specific representational models of ToM processing (Corradi-Dell'Acqua, Hofstetter, & Vuilleumier, 2014; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). For instance, Mason et al. (2008) compared stories requiring an inference about a character's intentions or emotional state and found rTPJ activation for intentions but not emotions. Similarly, Corradi-Dell'Acqua et al. (2014) demonstrated in a univariate analysis selective engagement of bilateral TPJ and pCC/PC when listening to stories about other's beliefs but not their emotions. The vmPFC was responsive to both belief and emotion stories. However, they found equivalent activation within these regions when making *judgments* about a character's belief or emotion. Moreover, they found high correlations between beliefs and emotion across the ToM network when using a multivoxel pattern analysis

(MVPA) approach. Variations between analytic approaches were also seen for Zaitchik and colleagues (2011) who found greater activation for mentalizing (belief/representation) relative to emotion in bilateral STS and IPL in an ROI analysis when adding mental state words (e.g. “thought”, “remember”, etc.) to the emotional sentences. In contrast to these past studies, several studies have shown no differences in the general ToM network between emotion and belief stories (Bruneau et al., 2012; Hynes, Baird, & Grafton, 2006). Hynes and colleagues (2006) found no differences comparing cognitive perspective taking and emotion perspective taking in the general ToM network (right TPJ, bilateral STS, dmPFC and mPFC), but observed some variation in lateral orbital frontal cortex and inferior frontal gyri. Bruneau and colleagues (2012) asked participants to (Task 1) rate the amount of pain felt by protagonists or (Task 2) actively empathize with the protagonist in stories of physical pain, emotional pain, or false beliefs and compared activation to matched control stories. They found generally similar activation patterns across tasks with greater activation in bilateral TPJ for empathizing. Importantly, they found that while emotional pain and false beliefs similarly activated the ToM network, physical pain stories activated an “empathy network” including insula, secondary sensory (supramarginal gyrus), middle frontal, and mid aCC all bilaterally (Decety & Lamm, 2007; Fan, Duncan, de Greck, & Northoff, 2011; Lamm, Decety, & Singer, 2011). Variation between emotional pain and physical pain was explored further by Bruneau and colleagues (2013) who analyzed cortical response to the same stories using an item-level regression approach with ratings of emotional pain, physical pain and vividness. Again, ratings of physical pain correlated with activation in the empathy

network, whereas emotional pain correlated with activation in the dorsal and ventral aspects of the mPFC and the pCC/PC region. In short, it is unclear how unique the neural network for understanding emotion is from other aspects of mentalizing and these effects may be driven by analytic method.

In the previous findings introduced, the degree to which the individual has to "infer" the emotion of the protagonist is confounded by several factors. In each of the studies above, the scenarios used explicitly mention the emotional state of the protagonist or combined story and judgment in the analyses eliminating the need for inferential processes with the exception of Corradi-Dell'Acqua et al. (2014) and Bruneau et al. (2012), however, both of these studies use mental or other (non-target) emotional state words in their stories. As such, the patterns of activation seen in these studies could equally reflect the response to emotion or mental state words without providing much insight into inferential process what a protagonist is experiencing. Furthermore, the previous studies have generally included a behavioral response specific to the emotion or mental state in the window of analysis (Beaucousin et al., 2007; Ferstl & von Cramon, 2007; Hynes et al., 2006; Zaitchik et al., 2011) with the exception of a few which separated the response period (Corradi-Dell'Acqua et al., 2014) or contained an unrelated response (e.g., respond when finished reading, Saxe & Powell, 2006). The inclusion of a response specific to the mental state/emotion may similarly engage regions artificially and not reflect a pure inferential process. For instance, it may be the case that activation of the amygdala is a product of such decision responses to affective stimuli as has been shown with viewing faces with affect (Pérez-Edgar et al., 2007), and may not be a product of the inferential process.

In summary, the literature on processing emotion from language has been limited to explicit references of emotion words either in the target statements (e.g., Corradi-Dell'Acqua et al., 2014; Zaitchik et al., 2011) or in a decision making component (Beaucousin et al., 2007; Ferstl & von Cramon, 2007; Zaitchik et al., 2011). Thus, it remains unclear what neural mechanisms are involved when one must actually infer the emotional state of others from situational contexts as described in language as opposed to explicitly being made aware of them. The question posed in our study is whether affective verbal utterances—lacking explicit lexical references of emotion and therefore necessitating inference—would recruit only regions associated with discourse processing or additional regions associated with mental state or emotional processing.

Present study

The aim of this investigation was to identify the underlying network of cortical regions involved in making inferences of affect from spoken discourse context. To achieve this goal, positive, negative and neutral scenarios (with natural but unaffected prosody) were presented to healthy participants during functional magnetic resonance imaging (fMRI). During the scan, subjects listened to the scenario then made a true-false (T/F) congruency judgment related to the emotion of the protagonist. Changes in the Blood Oxygenated Level Dependent (BOLD) contrast were analyzed on two periods. First, activations elicited by listening to the scenario and second, activations during the response period. While previous research has examined neural activations associated with emotional inferencing at the sentence/discourse level, to our knowledge this is the first to identify the effects of

positive and negative scenarios separately and which avoids the confound of explicit labels of emotion.

With respect to language processing systems in the brain, we hypothesized that listening to stories in all three conditions would elicit activations in regions involved in language comprehension, namely activation of medial frontal along with bilateral temporal and parietal regions (Ferstl & Neumann, 2008; Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mar, 2004; Prat, Mason, & Just, 2012). Additionally, given the previous findings of Ferstl and von Cramon (2005) as well as selected single word studies (Kensinger & Schacter, 2006; Maddock et al., 2003; Straube et al., 2011), we expected that emotional scenarios would involve areas consistent with processing emotions, i.e., bilateral amygdala, cingulate, and orbitofrontal cortices (reviews: Dolan, 2002; Phillips, Drevets, Rauch, & Lane, 2003; Wager, Phan, Liberzon, & Taylor, 2003). However, by temporally separating the cortical response to our decision probe from the story phase we can determine whether particular structures such as the amygdala are involved in the online inferential processing of emotion from the scenarios or if it is activated as a result of the decision-making process in which reference to emotion is explicit. Because all of our scenarios involve reflecting on the experience of a protagonist, we assume that all conditions (positive, negative and neutral) involve some degree of social processing. Thus, the resulting differences between conditions will reflect the influence of affect in the inferential process. Given previous behavioral research on affective word processing (Herrington et al., 2005; Kuchinke et al., 2005; Straube et al., 2011), we

predicted that the positive scenarios would evoke faster responses than the negative (compared to neutral).

Methods

Participants

Twenty-two native English speakers recruited from the greater Washington DC area contributed data to the present study (11M; mean age 21.3). Data from two individuals (and one run from one participant) were excluded due to low accuracy resulting in a final sample size of 20. All subjects reported being free of auditory deficits, neurological and major medical conditions, and had no history of head trauma (loss of consciousness of more than ten minutes and/or head injury). Participants also reported that they had no history of any substance dependence and were not currently medicated.

All participants completed the Edinburgh Handedness Inventory (Oldfield, 1971), and received behavioral assessments including the Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock, McGrew, & Mather, 2001), and two social measures: the Autism Spectrum Quotient (AQ)[3] (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) which is aimed at identifying symptoms or behaviors of autism in adults or adolescents of average intelligence, and the Social Responsiveness Scale (SRS) (Ingersoll,

[3] Findings from a recent systematic review of AQ since its inception in 2001 show AQ scores for nonclinical individuals: M = 16.94 (SD = .8 - 9.7), with males scoring slightly higher M = 17.89 (SD = 11.4 - 19.0) than females M = 14.88 (SD = 10.4 – 17.4). Scores for matched autism spectrum individuals: M = 35.19 (SD = 27.6 – 41.1), with males scoring slightly *lower* M = 36.40 (SD = 28.0 – 40.1) than females in this group M = 38.83 (SD = 31.9 – 42.5) (Ruzich et al., 2015). This is consistent with averages originally proffered by Baron-Cohen et al., (2001).

Hopwood, Wainer, & Brent Donnellan, 2011) completed by a family member or close friend, and designed to identify the presence and extent of autistic social impairment. (The former were administered as future plans include extending this paradigm to individuals with autism.) All study participants received a thorough explanation of the experimental procedures, and written consent was obtained in accordance with the requirements of the Institutional Review Board of University of Maryland. Subjects received monetary compensation for participation.

Task Procedures

Trial structure of the EIT is presented in Figure 2. A total of 72 passages with 24 positive, 24 negative and 24 physical state trials and a congruent and incongruent Target sentence for each were evenly distributed over four runs using an event-related paradigm (see Appendix B for details regarding stimuli production and selection, and Appendix C for EIT stimuli). The congruent and incongruent items were randomized such that each participant randomly received 12 congruent and 12 incongruent Target sentences per condition (positive, negative, and physical). Each run began with the display of a fixation cross for 500 msec, followed by the aurally-presented passage (~10-12 seconds). A blank screen followed for a duration that was jittered between 3-6 seconds. Then, the target sentence stating "He/She felt …" with a congruent or incongruent word was presented visually for 3 seconds during which a true or false congruency judgment was made via a button press. Each trial (from Cue to Target sentence) was presented for 16-18 seconds, with an inter-trial interval jittered 3-5 seconds. Participants were instructed to listen carefully to each scenario, and think about the feelings of the protagonist. They were told that they would then see a short

sentence, to which they would respond “true” or “false” by pressing a button on the response box. The tasks were implemented with MATLAB version 2010b (MATLAB, 2010), using the Psychophysics Toolbox extensions (Brainard, 1997).

Acquisition of Functional MR Data

Subjects were scanned using a Siemens 3T Trio MRI system with a 32-channel head coil. Functional images to estimate task-related activity were obtained with a gradient echo-planar imaging (EPI) sequence (repetition time=2000 msec, echo time=2400 msec, 64 × 64 matrix, flip angle 70°, FOV 192 mm). Whole brain coverage was obtained with 36 axial slices (thickness=3.2 mm; in-plane resolution=3.0 × 3.0 mm). A high-resolution T1-weighted MPRAGE scan (repetition time=1900 msec, echo time=2320 msec; field of view=230 mm; flip angle=9°; 192 sagittal slices; thickness=0.9 mm; 0.9 × 0.9 matrix) was obtained covering the whole brain.

Data Analysis

Analysis of behavioral data

Performance measures were accuracy and response time (calculated on correct trials only) to the EIT Target sentence recorded during fMRI acquisition. We examined the effect of valence and congruency on accuracy and response time separately with a two (group: congruent, incongruent) by three (valence: positive, negative, neutral) repeated measures analysis of variance (ANOVA). Post-hoc pairwise comparisons were Bonferroni corrected. Statistical analyses of behavioral data were performed using IBM SPSS (version 21.0).

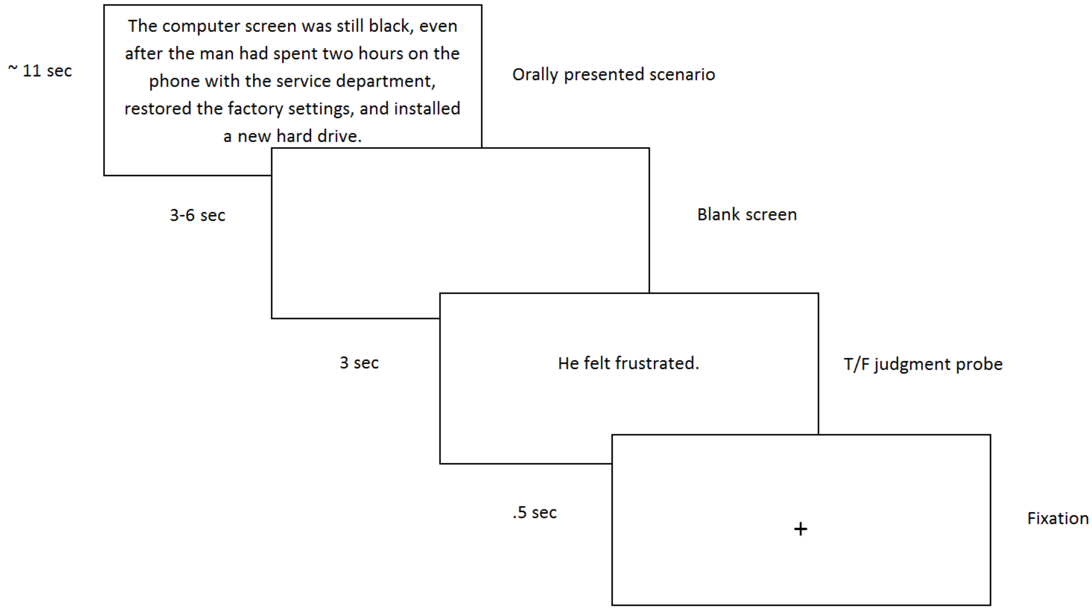


Figure 2. Experimental Design. 72 passages (24 each positive, negative, physical state) and a congruent and incongruent Target sentence were evenly distributed over 4 runs using an event-related paradigm. Congruent and incongruent items were randomized. Each run began with the display of a fixation cross for 500 msec, followed by the aurally-presented passage (~10-12 seconds). A blank screen followed for a duration that was jittered between 3-6 seconds. Then, the Target sentence "*He/She felt …*" with a congruent or incongruent word was presented visually for 3 seconds during which T/F judgment was made via a button press. Each trial was presented for 16-18 sec; inter-trial interval jittered 3-5 sec.

Analysis of functional MR data

Data analysis was performed using Statistical Parametric Mapping (SPM12b, http://www.fil.ion.ucl.ac.uk/spm). Preprocessing of the EPI time series included: (1) realignment for head motion correction, (2) spatial normalization into the Montreal Neurological Institute (MNI) anatomical space, and (3) spatial smoothing (6mm FWHM). Data were high pass filtered at 128 Hz, and examined for excessive motion and spiking artifacts using the Artifact Detection Tool (ART) software package. Outliers in the image time series (Z-threshold: 3.0, scan to scan movement threshold

1.0 mm) were identified and excluded from subsequent statistical analysis (4.6% of the data).

For each participant, a general linear model (GLM) was used to estimate the parameters for the stories and probe separately. The story model included three story factors: positive (“POS”), negative (“NEG”), and neutral (“NEUT”) as well as a factor for each of the two probe conditions, congruent and incongruent. In order to evaluate the effect of response time (RT), an additional model including individual RT times as a parametric modulator for each of the probe conditions was employed. All factors were convolved with a canonical hemodynamic response function (Friston, Frith, Turner, & Frackowiak, 1995). Six realignment parameters as well as outlier time points were included in the models as regressors of no interest. The contrast images from the first level analyses were then subjected to second level random effects analyses.

To determine regions of increased task-related signal change for the overall effect of listening to stories (POS+NEG+NEUT) relative to the implicit (fixation) baseline at the group level, we performed a one-way ANOVA and reported the overall effects of condition. To examine the effect of valence, whole brain analysis of stories was performed using a within subjects repeated measures design. The main contrasts of interest were the effect of emotion compared to neutral (POS+NEG vs. NEUT) as well as the individual contributions of NEG vs. NEUT and POS vs. NEUT. Effects of valence were further measured by comparing POS vs. NEG and NEG vs. POS.

Whole brain analysis of the probe was performed using *t*-tests for the event-related response to the congruent and incongruent conditions. An additional first-level model was conducted using item-level RT as a parametric modulator for condition effects on the probe (Grinband et al., 2011). As a factor, RT did not account for any activation in cortex. There was little difference in activation patterns with the addition of RT compared to the original, thus the analyses reported are those without the modulator. As behavioral results did not reveal statistically significant differences between conditions of valence, the main contrasts of interest were congruent and incongruent items separately. Whole brain contrasts were corrected at FWE $p < 0.05$.

Results

Behavioral Results

A 2 (CON, INCON) x 3 (POS, NEG, NEUT) repeated measures ANOVA for response times to correct trials (RT) revealed a significant main effect for valence $F(1.444, 27.431) = 30.126$, $p < .001$. Contrasts revealed that RTs to POS stories $F(1, 19) = 52.193$, $p < .001$, $r = .86$, and NEG stories $F(1, 19) = 8.996$, $p = .007$, $r = .57$, were significantly faster than NEUT stories. There were no significant differences between RTs to POS and NEG stories. There was also a significant effect of congruency $F(1, 19) = 9.189$, $p = .007$. RTs were significantly longer for INCON than CON trials. Accuracy scores were also subjected to a factorial repeated-measures ANOVA. There was a significant main effect of valence $F(1.252, 23.796) = 4.01$, $p = .049$. Contrasts revealed that accuracy to POS $F(1, 19) = 7.168$, $p = .015$, $r =$

.52, was significantly better than NEUT; no significant differences were revealed for accuracy between the other conditions. See Table 3 for results.

Table 3.

Behavioral results, Study 1

Condition	Response time in msec Mean (SD)	Response time in msec Standard error	Accuracy % correct Mean (SD)	Accuracy % correct Standard error
PosCon	1164.67 (280.66)	62.72	98.75 (3.35)	.75
PosIncon	1228.31 (297.88)	66.61	98.74 (2.40)	.54
NegCon	1316.06 (243.86)	51.21	96.65 (5.18)	1.16
NegIncon	1320.83 (303.28)	67.82	96.45 (4.14)	.93
NeutCon	1351.70 (330.08)	73.83	97.48 (3.94)	.88
NeutIncon	1570.82 (309.98)	69.11	95.40 (6.33)	1.42

Note. Response time (RT) and accuracy results. 72 stories were distributed over 3 conditions of valence (36 positive, negative and neutral) and congruency (18 congruent and incongruent. Values are reported as mean, standard deviation (*SD*) and standard error. RTs are reported in milliseconds.

Functional MRI Results

Stories

The overall effect of processing verbal scenarios was determined by collapsing across positive, negative and neutral stories. As depicted in Figure 3A (and Appendix D, Table 1), the analysis revealed activation in left inferior frontal (triangularis) and both dorsal and ventral aspects of medial frontal cortex. There were also broad areas of significant activity in both temporal lobes, extending from posterior superior temporal gyri (pSTG) to the anterior temporal poles (aTP), and including bilateral fusiform and right inferior temporal gyri. In addition, significant activation was found in areas of the parietal lobe comprised of bilateral postcentral and right angular gyri and in the occipital cortex including right superior- and middle occipital gyri and a cluster including cuneus and lingual gyrus on the left. Subcortical

activation including right hippocampus, left middle cingulate and bilateral calcarine was found. The cerebellum also showed extended bilateral activation.

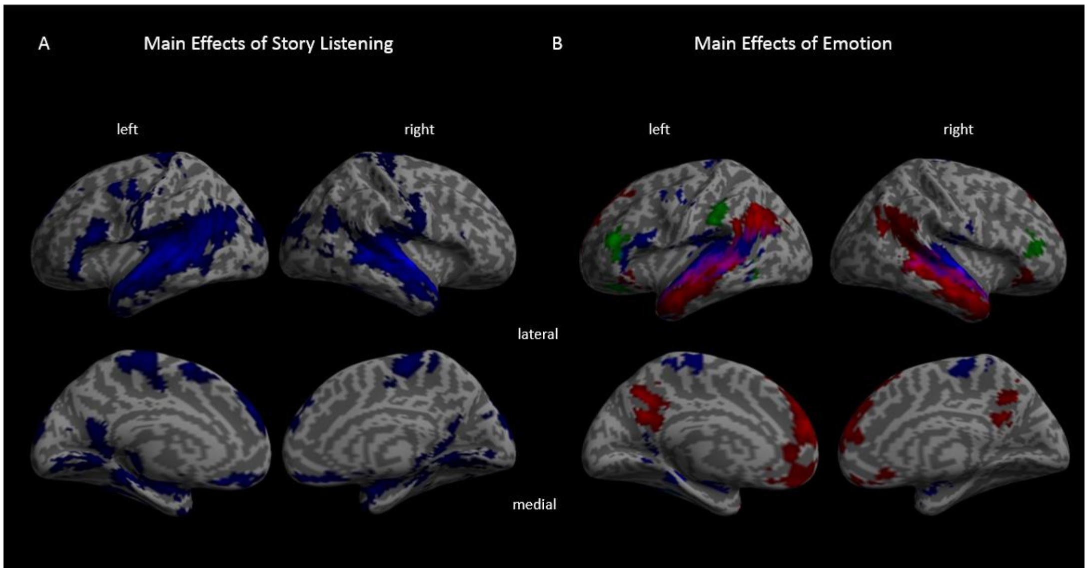


Figure 3 Activation maps illustrating the presence of significant functional activity associated with listening to stories. A) We show *t*-values for regions showing signal increases for the average effect of stories (POS + NEG + NEUT) vs. baseline contrast. B) We show *t*-values for signal increases associated with effect of emotion (POS + NEG) vs. NEUT in red, neutral vs. emotion in green, and neutral vs. baseline in blue. Regional variations in task-related activity are displayed using a threshold of $p < .001$ corrected with cluster extent FWE threshold ($p<0.05$) for *t*-statistic maps.

Emotion

To examine the contribution of emotion to the overall effect, we compared emotional stories (collapsing across positive and negative) to neutral stories (Table 4). As shown in Figure 3B, medial frontal areas (dmPFC, vmPFC and orbital frontal gyrus), pCC)/PC, bilateral angular and temporal gyri, and right inferior temporal gyrus had significantly greater activation for emotion relative to neutral stories. Interestingly, the analysis also revealed clusters of activation that were greater to neutral relative to emotional stories located in left inferior frontal gyrus (IFG; triangularis) and supramarginal gyrus. These activations are adjacent to, but isolated

from areas activated by the stories in general (Figure 3A) and the neutral stories relative to the implicit baseline (Figure 3B in blue)[4]. Parameter estimates for the story conditions at these clusters revealed that the contrast is a result of deactivation of these regions to emotional stories (both positive and negative, see bar plots Figure 4).

Valence

To further investigate the effects of emotion, we examined the contribution of POS and NEG through whole brain contrasts comparing NEG vs. NEUT and POS vs. NEUT. NEG < NEUT revealed greater activity in both dorsal and ventral mPFC, right inferior frontal gyrus, and large extents of activation along the superior temporal sulci bilaterally encompassing the anterior temporal poles, mid temporal cortex (including STG and MTG) extending to the temporal parietal junction (TPJ) (including angular gyri). Similarly, POS > NEUT elicited activation along the STS bilaterally including the aTP, STG, MTG and peaks in left angular gyrus, pCC/PC and additionally in mPFC, where activation was greater compared to the NEG > NEUT contrast (see Figure 4 images). Table 5 presents results of individual contrasts from the repeated-measures ANOVA. As many of the areas sensitive to valence are overlapping, we extracted the intensity of activation in selected regions of interest described above. Figure 4 (surrounding graphs) shows that the effects of both positive and negative valence were quite similar, and were stronger than neutral valence in all regions. In a direct comparison of POS and NEG valence, the regions that survived corrected threshold were the MTG for NEG > POS and the pCC for POS > NEG.

[4] Note that right IFG also appears to be significant for neutral stories in Figure 4B, but does not appear in Table 5. This is due to the figure showing activation at an uncorrected voxel level threshold ($p<0.001$) but a cluster corrected threshold (FWE<0.05) whereas the table on included peaks with voxel-wise corrected thresholds (FWE $p<0.05$).

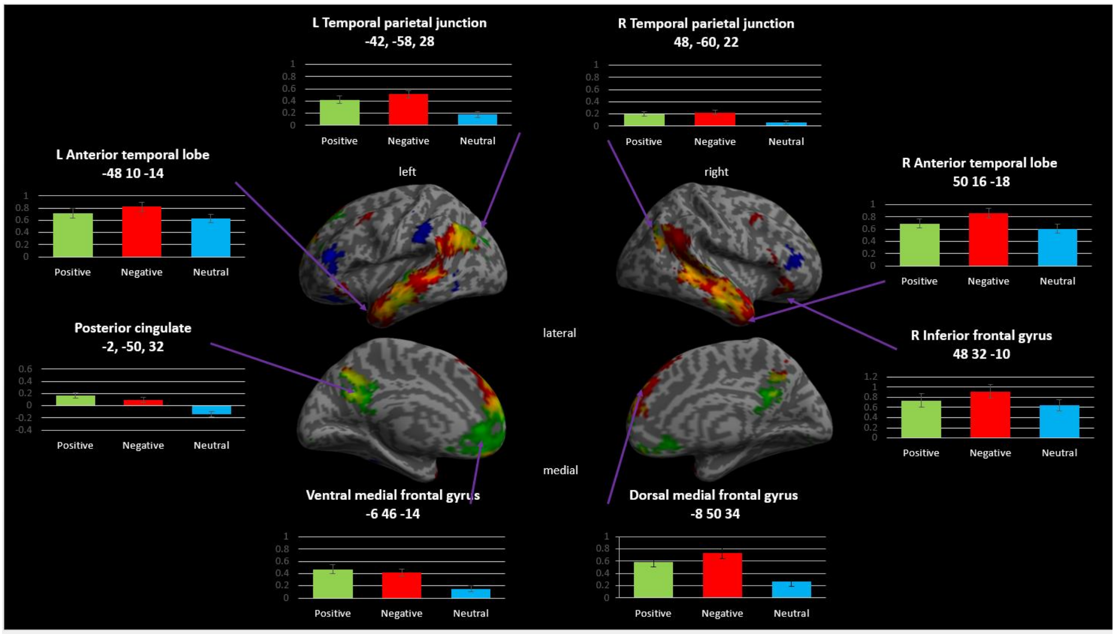


Figure 4. Activation maps illustrating the presence of significant functional activity associated with valence; effect of positive vs. neutral is shown in green, negative vs. neutral is shown in red, and neutral vs. emotion (positive + negative) is shown in blue. Yellow indicates areas of overlap. Regional variations in task-related activity are displayed using a threshold of $p < .001$ cluster corrected for t-statistic maps. Error bars show standard error.

The effects of NEUT stories contrasted with both NEG and POS was also examined using individual contrasts from the repeated measures ANOVA. These contrasts showed that NEUT > NEG stories revealed two left frontal peaks, superior orbital gyrus and IFG (triangularis), as well as significant activity in supramarginal gyrus. As discussed in the contrast of NEUT > POS+NEG, this effect is the result of deactivation to emotional stories. The comparison of NEUT > POS showed nearly identical peaks (to that of NEUT > NEG) in both superior orbital gyrus and IFG.

Decision-making response

To investigate the effect of RT, we calculated a one-sample *t*-test for the event-related response to the CON and INCON conditions with individual RT as a

covariate. Results for RT were not significant, suggesting that the effects can be attributed to the condition of congruency and not to task difficulty. Several areas were activated for both the CON and INCON (compared to baseline), including left- aTP, inferior temporal gyrus, angular gyrus, and right insula. Common bilateral activations were found in IFG, putamen, occipital area and cerebellum. Additional significant peaks related to the CON condition included right aTP, and left MTG, insula, Heschl's gyrus, postcentral gyrus, insula and thalamus. Peaks of significant activation for the INCON condition included SFG, right MTG, as well as bilateral amygdala, right caudate and left hippocampus (Figure 5 and Appendix D, Table 2).

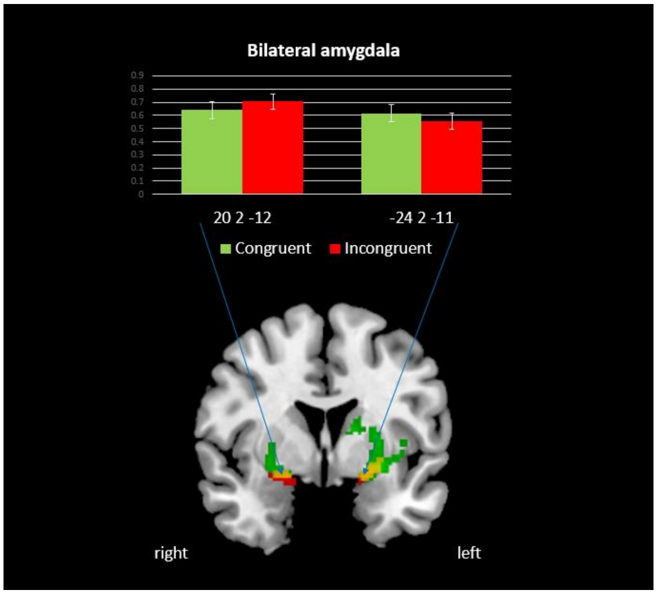


Figure 5. T/F response results. Activation maps illustrating the presence of significant functional activity in subcortical areas associated with probe; effect of CON is shown in green, INCON is shown in red; areas of overlap are yellow. Regional variations in task-related activity are displayed using a corrected threshold of $p < .05$ FWE for *t*-statistic maps.

Table 4.

Brain activity associated with EMO and NEUT stories, Study 1

Region label	Left					Right				
	x	*y*	*z*	*t*	*d*	*x*	*Y*	*z*	*t*	*d*
Emotion > Neutral										
Frontal										
vmPFC	-2	38	-22	7.48	3.16					
	-4	42	-20	7.17	2.67					
dmPFC	-10	54	38	8.73	4.00	6	52	20	7.65	3.51
	-8	56	22	7.92	3.63	4	50	44	6.74	3.09
	-2	58	36	6.52	2.99					
	-4	60	10	6.40	2.94					
Temporal										
STS	-60	-16	-6	8.62	3.95	52	-6	-12	7.65	3.51
MTG	-54	-12	-12	9.91	4.55	58	-18	-10	10.24	4.70
	-52	-2	-26	8.82	4.05	64	-10	-18	9.03	4.14
	-52	-20	-12	8.56	3.93	48	-34	0	8.76	4.02
	-56	-2	-24	8.55	3.92	56	-38	0	8.41	3.86
	-52	-36	-2	7.95	3.65	58	-34	-2	8.25	3.79
	-50	-6	-20	7.71	3.54	50	-6	-20	8.23	3.78
	-64	-16	-14	7.67	3.52	50	-2	-22	8.12	3.73
	-56	-30	-6	6.69	3.07	58	-36	-8	7.86	3.61
						58	4	-26	7.58	3.48
						50	4	-22	7.56	3.47
						58	-4	-10	7.36	3.38
						52	-60	24	6.23	2.86
Middle temporal pole	-54	8	-30	9.05	4.15	46	12	-28	7.98	3.66
						46	20	-28	7.06	3.24
ITG	-50	0	-30	8.04	3.69					
Parietal										
Supramarginal gyrus						62	-54	26	6.39	2.93
Angular gyrus	-60	-60	28	8.84	4.06	56	-62	32	6.46	2.96
	-42	-58	28	8.80	4.04					
	-48	-60	32	8.70	3.99					
Subcortical										
aCC	-4	52	20	8.18	3.75					
	-8	50	18	7.98	3.66					
mCC	-2	-52	34	10.22	4.69					
Precuneus	-2	-58	26	7.55	3.46					
Cerebellum										
Cerebellum crus I	-20	-76	-34	8.21	3.77					
	-20	-82	-28	7.17	3.29					
Cerebellum crus II	-28	-80	-34	7.48	3.43	24	-76	-34	6.72	3.09
	-16	-84	-36	6.46	2.97					
Neutral > Emotion										
Frontal										
vmPFC	-22	32	-16	9.42	4.32					
IFG (tri)	-42	36	14	8.23	3.78					
Parietal										
Supramarginal gyrus	-64	-28	28	7.5	3.44					

-60	-32	44	6.2	2.84

Note. We show *t*-values for signal increases associated with emotion using Positive + Negative vs. Neutral, signal increases associated with neutral using Neutral vs. Positive + Negative. Coordinates are MNI space. Height threshold: $t = 6.14$, $P < .05$, FWE corrected. Extent threshold: $k = 0$ voxels.

Discussion

Our aim was to understand the neural mechanisms supporting emotional inferences made from discourse context without direct references of emotion from verbal ("sad, happy, and mad") or non-verbal (prosody, facial expression) cues. To do this, we used vignettes devoid of overt emotional words or prosody, such that listeners were required to infer the protagonist's emotion using linguistic information only. Although previous studies have examined the neural correlates related to inferring emotion from language (Beaucousin et al., 2007; Corradi-Dell'Acqua et al., 2014; Ferstl et al., 2005; Ferstl & von Cramon, 2007; Mason, Williams, Kana, Minshew, & Just, 2008), to our knowledge this is the first to investigate the neural correlates related to processing scenarios of positive, negative and neutral valence separately without explicit use of emotion words. In addition, we analyzed the BOLD response to the verbal scenarios and response periods separately, allowing us to differentiate between neural activations during the period of inference from those concerned with explicit judgments of emotion or decision making in general.

Table 5.

Brain activity associated with valence, Study 1

Region label	Left					Right				
	x	*y*	*z*	*t*	*d*	*x*	*y*	*Z*	*t*	*d*
Negative > Neutral										
Frontal										
vmPFC	-2	40	-22	6.29	2.04					
dmPFC	-4	52	22	8.40	2.73	6	52	20	8.09	2.62
	-2	46	32	6.53	2.12	6	50	42	7.0	2.27
	-2	58	36	6.29	2.04	6	42	36	6.47	2.10
mPFC	-10	54	38	8.27	2.68					
IFG						48	32	-10	6.33	2.05
Temporal										
STS	-42	-58	28	8.58	2.78					
	-68	-50	20	6.70	2.17					
	-68	-44	4	7.07	2.29					
	-44	14	-22	6.92	2.25					
MTG	-54	8	-30	10.29	3.34	52	-22	-12	11.37	3.69
	-54	-12	-12	10.03	3.25	58	-18	-10	10.85	3.52
	-54	-36	-2	9.55	3.10	48	-34	0	9.64	3.13
	-52	-2	-26	9.30	3.02	56	-34	-4	9.33	3.03
	-52	-22	-10	9.06	2.94	50	6	-22	9.11	2.96
	-58	-30	-6	8.43	2.74	58	-38	0	8.96	2.91
	-60	-16	-6	8.21	2.66	50	-2	-22	8.87	2.88
	-54	2	-18	7.83	2.54	64	-14	-16	8.38	2.72
	-46	-42	0	7.20	2.36	54	-6	-12	8.21	2.66
	-68	-44	4	7.07	2.29	54	-4	-10	8.16	2.65
	-64	-16	-14	6.64	2.15	52	-30	-8	8.07	2.62
						48	6	-30	7.96	2.58
						56	6	-26	7.89	2.56
						60	2	-14	7.87	2.55
Middle temporal pole	-60	6	-16	6.75	2.19	46	12	-28	9.23	2.99
						48	18	-26	8.24	2.67
Parietal										
Inferior parietal						52	-46	28	6.38	2.07
Angular gyrus	-60	-60	28	9.58	3.12	56	-62	32	7.10	2.30
	-48	-58	30	8.65	2.81	62	-54	32	6.86	2.23
						44	-50	24	6.68	2.17
Subcortical										
Precuneus	-4	-54	34	7.79	2.53					
Cerebellum										
Cerebellum lob VIIa crus I	-20	-76	-34	9.23	2.99	24	-82	-30	7.22	2.34
	-20	-82	-28	7.71	2.50	26	-76	-34	7.15	2.32
Neutral > Negative										
Frontal										
vmPFC	-22	34	-16	9.05	2.94					
IFG (tri)	-40	36	14	8.08	2.62					
Parietal										
Supramarginal gyrus	-64	-28	28	7.25	2.35					
	-60	-32	44	6.83	2.22					
	-54	-30	40	6.34	2.06					
Positive > Neutral										
Frontal										

vmPFC	-6	46	-4	6.29	2.04				
	-4	38	-22	6.27	2.03				
dmPFC	-10	54	38	7.0	2.27				
	-4	60	10	6.86	2.23				
	-8	56	22	6.81	2.21				
	-10	52	20	6.59	2.14				
Temporal									
MTG	-52	-14	-16	7.57	2.46	64	-10	-18	8.14
	-60	-14	-8	6.89	2.24	58	-18	-10	6.99
	-64	-16	-14	6.83	2.22	44	-44	4	6.61
	-56	-2	-24	6.80	2.21	50	-6	-20	6.17
Parietal									
Angular gyrus	-42	-58	28	6.81	2.21				
	-46	-60	32	6.77	2.20				
Subcortical									
pCC	-2	-50	32	10.76	3.49				
	-2	-46	30	10.48	3.40				
Precuneus	-2	-58	26	7.64	2.48				
Neutral > Positive									
Frontal									
vmPFC	-22	32	-16	7.70	2.50				
IFG (tri)	-42	36	14	6.53	2.12				
Negative > Positive									
Temporal									
MTG	-56	-34	-4	6.69	2.17	52	8	-20	6.3
Positive > Negative									
Subcortical									
Cuneous	-12	-72	34	6.77	2.20				
mCC						8	-30	32	6.16

Note. We show *t*-values for signal increases associated with valence using four contrasts from repeated measures ANOVA: Negative vs. Neutral, Neutral vs. Negative, Positive vs. Neutral, Neutral vs. Positive, Negative vs. Positive and Positive vs. Negative. Coordinates are MNI space. Height threshold: $t = 6.14$, $P < .05$, FWE corrected. Extent threshold: $k = 0$ voxels.

Our primary hypothesis argued that emotionally valent stories would activate regions associated with social-affective processing in addition to regions associated with discourse processing and inference making in general. Our findings revealed that the set of cortical regions more responsive to emotional relative to neutral stories generally overlap with regions activated by the neutral stories (see Figure 4B) suggesting that emotional stimuli enhances activation in regions responsive to discourse. This set of regions surrounding the mid-section of the STS bilaterally and extends toward the temporal poles has been repeatedly shown to be engaged in

narrative processing (Ferstl & Neumann, 2008; Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mar, 2004, 2011; Prat, Mason, & Just, 2012). As shown in meta-analyses of narrative processing (Ferstl & von Cramon, 2007; Mar, 2011), these regions are engaged irrespective of the inclusion of human characters or mentalizing processes in the stories themselves. These regions are also engaged whether the stories are presented auditorally or visually (Hickok & Poeppel, 2007; Jobard, Vigneau, Mazoyer, & Tzourio-Mazoyer, 2007). As shown by Mar's (2011) meta-analyses (see Figure 6), the mid STS and temporal poles are engaged in studies of ToM whether they are story based or not. Beyond the network associated with neutral stories, the emotionally valent stories elicited activation in medial and orbital prefrontal regions as well as bilateral temporal parietal junction/superior temporal gyri and precuneus/pCC. These findings are consistent with the hypothesis that inferring the emotional state of another engages regions associated with mentalizing, or ToM, as all of these regions are part of the putative ToM network (Frith & Frith, 2003; Gallagher & Frith, 2003; Saxe & Kanwisher, 2003; Saxe & Powell, 2006).

Contrary to our hypotheses, we did not find greater activation for emotional stimuli in the insula, dorsal aCC, or amygdala, regions traditionally associated with emotion processing and empathy (Decety & Lamm, 2007; Fan et al., 2011; Lamm et al., 2011). To the contrary, the contrast of neutral relative to emotional stimuli showed greater activation in IFG and supramarginal gyrus (SMG) bilaterally which tend to be associated with empathy for physical pain (Bruneau et al., 2013; Bruneau et al., 2012) or bodily sensations (Saxe & Powell, 2006). Given the nature of the neutral stimuli which reflected more physical states of hunger, fatigue, or body

temperature, the engagement of secondary somatosensory regions (SMG) and IFG regions just anterior to the insula suggests that these components of the empathy network are reflective of the physical, rather than emotional nature of the empathy response. Thus, our contrast of emotional relative to neutral stimuli reveals greater engagement of the network of regions associated with language and mentalizing, whereas the inverse contrast engages areas involved in empathy for physical sensations.

Narrative processing or mentalizing networks

Our theoretical aim was to determine whether drawing inferences regarding the emotion of another person is reflected in cortical regions beyond the language network. However, it is unclear exactly how unique the networks for language processing and mentalizing (Deen, Koldewyn, Kanwisher, & Saxe, 2015; Ferstl & von Cramon, 2001; Mar, 2011; Spreng & Mar, 2012). For instance, Figure 6 shows the spatial overlap in activation patterns reported in one meta-analysis conducted on studies of narrative processing (red) and studies of mentalizing or ToM in the context of stories (dark blue; Mar, 2011). The remarkable amount of overlap in the networks particularly along the STS (particularly, the TPJ and ATL), the dorsal and ventral medial prefrontal cortex (mPFC) and insula bilaterally suggests common underlying processes involved in these domains (Deen et al., 2015; Redcay, 2008). Whereas some have suggested the common patterns of activation are indicative of processes of mental simulation of the thoughts and perspective of others (Mitchell, Banaji, & Macrae, 2005; Mitchell, 2009; however see Saxe, 2005), others have similarly argued that processes of retrospective and prospective memory that are required for

understanding the goals and intentions of others are invoked (Buckner & Carroll, 2007; Schacter, Addis, & Buckner, 2007; Spreng & Grady, 2009; Spreng, Mar, & Kim, 2008) or that these networks reflect the control of cognition from externally modulated toward internal mental processes (Corbetta, Patel, & Shulman, 2008). It has also been argued that processes of ToM and narrative inferencing may independently activate a region such as mPFC (Ferstl & von Cramon, 2002) or that subnetworks such as a medial (mPFC and pCC system) modulate mental/emotional reactivity (Bruneau et al., 2013; Ochsner, Bunge, Gross, & Gabrieli, 2002), whereas the lateral network (bilateral TPJ) reflects a cognitive appraisal of the situation (Decety & Lamm, 2007; Mars et al., 2012). Despite the competing theories, it is necessary to determine the networks involved when actually inferring a protagonist's emotional state absent of the potentially confounding elements of explicit mental/emotional state words and task response. Whereas previous studies of emotional processing of scenarios have generally found engagement of the ToM network including bilateral TPJ, STS, and medial regions including dmPFC, vmPFC, and pCC/PC (Bruneau et al., 2012; Corradi-Dell'Acqua et al., 2014; Hynes et al., 2006; Zaitchik et al., 2011), most of these studies have focused on negative affect of painful experiences or did not account for the effects of valence.

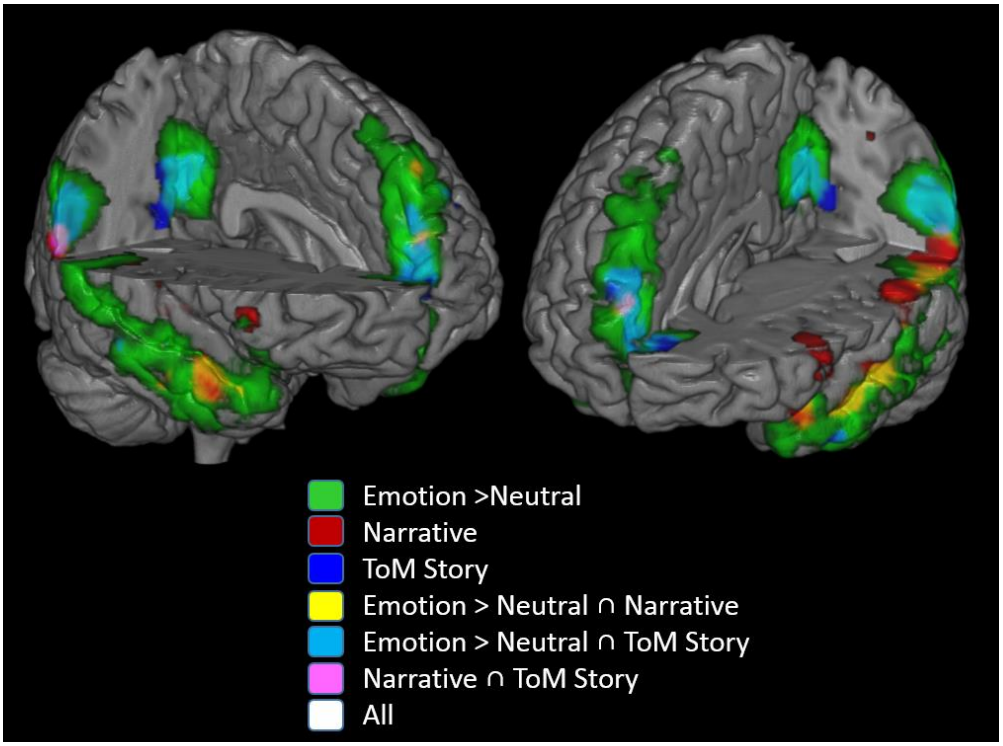


Figure 6. Emotion (EMO) > neutral (NEUT) activation (green) shown together with regions associated with narrative comprehension (NARR; Mar, 2011; red), ToM stories (TOM; Mar, 2011; dark blue), areas where (EMO > NEUT) ∩ NARR (yellow), (EMO > NEUT) ∩ TOM (light blue), NARR ∩ TOM (pink) and the overlap of all (white). Regional variations in task-related activity are displayed using a threshold of $p < .001$ corrected with cluster extent FWE threshold ($p<0.05$) for t-statistic maps.

Effects of valence

The direct comparisons of positive and negative valence at the stringent voxelwise correction threshold reported in Table 5 revealed that negative stories produced greater activation in the left lateral MTG/STS region whereas positive stories yielded greater activation in the mid/posterior cingulate region. However, when looking at these conditions relative to baseline, as in Figure 4, a clear pattern is revealed in which negative stimuli more strongly activate the lateral temporal regions and the dorsal aspect of mPFC (Figure 4 in red) whereas positive stories are more associated with the pCC and ventral aspect of the mPFC. Specifically, there is a

significant cluster in the ventral aspect of the medial orbital frontal area (xyz = -8, 60, -4) for positive versus negative stories, whereas the negative versus positive contrast reveals a cluster located more dorsally in the frontal superior medial region. When using a clusterwise correction (FWE $p<0.05$) for voxels at the uncorrected $p<0.001$ threshold (Figure 7) it is clear that there is greater activation for negative relative to positive stories in the TPJ regions bilaterally and along the mid-STS extending down toward the ATLs in addition to the dmPFC. Moreover, the positive stories show greater activation in the posterior medial regions including the pCC/PC and neighboring posterior parietal and cuneus region in addition to the vmPFC region.

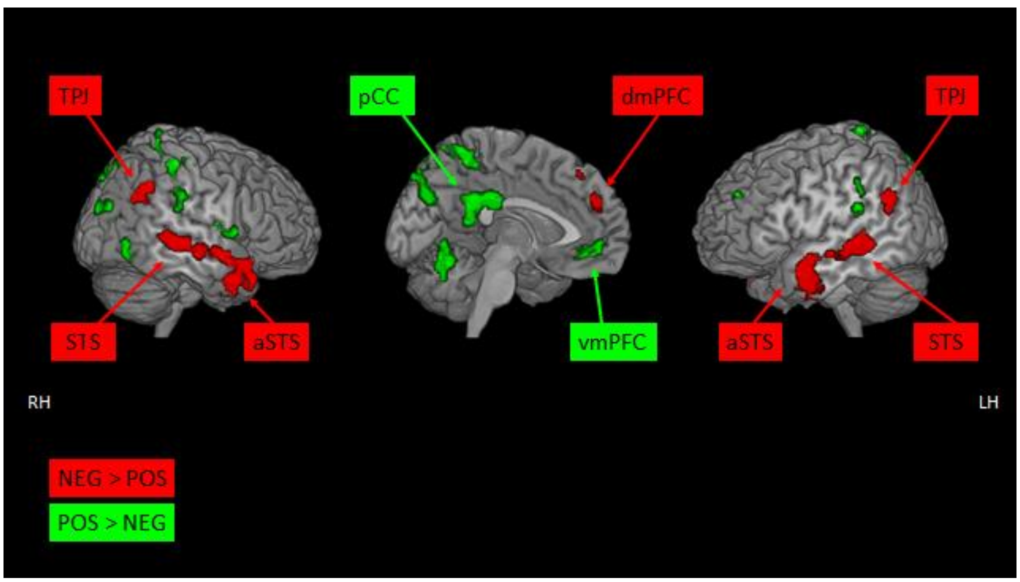


Figure 7. Contrasts of negative compared to positive (NEG > POS; red) and POS > NEG (green). Regional variations in task-related activity are displayed using a threshold of $p<.001$ corrected with cluster extent FWE threshold ($p<0.05$) for t-statistic maps.

With respect to the putative TOM and NARR networks discussed, positive stories are generally associated with the vmPFC and pCC, both of which are associated with the ToM network shown in Figure 6. In general, the pCC activation

across conditions revealed deactivation for neutral items and more positive activation for emotional items with positive stimuli being most active (see bar plot in Figure 4). As discussed, the pCC (in conjunction with the mPFC and TPJ) has been implicated as part of the brain's default mode network (DMN) which is often shown as anti-correlated with task demands and the cognitive control system (Fox et al., 2005). Based upon our behavioral results, it appears that our neutral condition was more difficult than the emotion conditions with respect to the EIT task and thus the pCC activity, and the similar pattern in vmPFC, could reflect effort in cognizing (the DMN explanation). On the other hand, the pCC has also been associated with the processing of pain and emotion (Maddock & Buonocore, 1997; Maddock et al., 2003), ToM (Saxe & Powell, 2006), and self-referential and other-referential processing (Spreng & Grady, 2009). Interestingly, meta-analyses reveal slight spatial variation in the pCC for investigations of memory relative to pain, and the invocation of emotion and cognitive effort is topographically indistinct (Nielsen, Balslev, & Hansen, 2005). Together with regions of the dmPFC, the pCC has been proposed to invoke episodic traces in the service of retrospective memory or prospective construction of scenarios (Buckner & Carroll, 2007; Schacter et al., 2007; Spreng & Grady, 2009; Spreng et al., 2008). Because the neutral stimuli in our study also engages these episodic traces, simulation alone does not account for the greater activation for emotional stories. Similarly, the vmPFC has been implicated in discourse processing (Ferstl & von Cramon, 2002) and in processing emotional words (Beauregard et al., 1997; Maddock et al., 2003; Maratos et al., 2001), higher level inferencing of emotional discourse (Beaucousin et al., 2007; Corradi-Dell'Acqua et al., 2014; Ferstl et al., 2005) as well

as self-referential processes and reasoning about another person's thoughts (Ferstl & von Cramon, 2002; Frith & Frith, 1999; Gallagher & Frith, 2003). More interestingly, the contrast between positive and negative valence within our stories revealed a differentiation in activation in the dorsal and ventral aspects of mPFC. These findings are consistent with a recent meta-analysis showing that the dorsal medial PFC is more active in response to negative feedback while the orbital/ventral PFC is more responsive to positive feedback and social acceptance (Crone, 2014). According to Crone, the connections to the dorsal mPFC from the dorsal anterior cingulate (daCC) and the supplementary motor area (SMA) serve as a negative feedback loop in social and cognitive functioning, whereas the ventral mPFC has more direct connections with the reward system in the subgenual aCC and ventral striatum and responds to positive social-affective feedback.

In addition to the dorsal aspect of the mPFC, the negative stories are also associated with bilateral TPJ, ATL, and STS all of which are regions that show relative overlap between narrative processing (NARR) and mentalizing (TOM). Bilateral posterior temporal/parietal (TPJ) regions were significantly more active for stories eliciting emotional inferences compared to stories eliciting inferences about bodily states. These findings are consistent with a role for this region in narrative comprehension as well as inferences of others' mental or emotion state above and beyond narrative comprehension alone (Beaucousin et al., 2007; Deen et al., 2015; Mar, 2011; Saxe & Kanwisher, 2003; Saxe & Powell, 2006). While our results are at odds with others who have shown that TPJ activation is related to mental/belief states but not emotional states (Mason et al., 2008; Zaitchik et al., 2011), the fact that

negative scenarios had greater activation than even positive suggests that this region is not only responsive to emotion, but also to valence. This is consistent with recent findings from Bruneau et al (2012) who found greater activation to emotionally painful stories relative to non-painful (yet emotional) stories. Our findings are also consistent with Saxe and Powell (2006), who showed the bilateral TPJ was activated for the processing of others mental states, but not their bodily sensations or appearance. The content of our neutral items included bodily sensations such a fatigue and hunger that may be more akin to their "non-mental" manipulations. This study extends these findings to demonstrate that inferences about emotional states (without reference to beliefs or desires) engage the TPJ to a greater extent than non-mental bodily states.

Negatively valent stories engaged the anterior temporal lobes (aTL) bilaterally to a greater extent than positive stories. In studies of discourse processing, there is strong evidence for involvement of the aTLs for language comprehension in general (Ferstl & Neumann, 2008), and more specifically for semantic integration over sentences and texts (see Stowe, Haverkort, & Zwarts, 2005 for review). However, findings of emotional valence in the aTL have not been documented previously. Other lines of research implicate the aTL for ToM processes (Frith & Frith, 2003; Gallagher & Frith, 2003) and for making inferences about others' emotional state (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Maratos et al., 2001; Völlm et al., 2006). In fact, Völlm and colleagues (2006) showed overlapping areas of activation in aTLs for empathy and theory of mind tasks. A recent review proffers the suggestion that the aTL are, "sensitive to stimuli that tell a story . . . and to tasks that

require one to analyze other agent's emotions, intentions or beliefs" (Olson & Plotzker, 2007). Our data are consistent with past findings and extend them to demonstrate that aTL plays a role in making emotional inferences from sentence context without explicit lexical reference to the emotion. This effect appears to be enhanced for negatively valent stimuli. Thus, as with the dmPFC and TPJ, the aTL likely plays a role in the evaluation of emotionally-relevant mental states conveyed through linguistic stimuli beyond the semantic information.

Effects of decision making in EIT task

Based on previous studies of processing emotion in language (Beaucousin et al., 2007; Ferstl et al., 2005), we hypothesized that the amygdala would be involved in the inferential process. While we did not see subcortical activity in the amygdala and striatum during the story phase, this region was engaged in the context of the true/false congruency judgment including the putamen, caudate, insula and amygdala (see Figure 5 and Appendix D, Table 2). This is consistent with research that has shown that the striatum is centrally involved in decision-making processes (Balleine, Delgado, & Hikosaka, 2007), particularly those involving a social component (Rilling et al., 2002; Sanfey, 2007). Emotional processes, too play a role in decision-making (Grecucci, Giorgetta, van't Wout, Bonini, & Sanfey, 2013; Naqvi, Shiv, & Bechara, 2006). This may explain why, in contrast to previous studies of emotional words (Maddock et al., 2003; Maratos et al., 2001; Nakic et al., 2006; Straube et al., 2011) and stories (Beaucousin et al., 2007; Ferstl et al., 2005), our emotional vignettes failed to elicit amygdala activations. Each of these studies included a) explicit

references to emotion or b) a response condition, suggesting that previous findings were due to decision making factors on emotion (Pérez-Edgar et al., 2007).

Conclusion

The present study extends previous research on inferential processing of emotional language (Beaucousin et al., 2007; Bruneau et al., 2013; Bruneau et al., 2012; Ferstl et al., 2005; Ferstl & von Cramon, 2007) by differentiating positive and negative emotion, and also by examining the BOLD response to vignettes separately from the response condition. We showed that verbal emotional stimuli enhances activation of cortical regions generally responsive to discourse, and also regions associated with affective processing and social cognition, specifically medial and orbital frontal regions, bilateral middle temporal areas, temporal parietal junction/superior temporal gyri and pCC/PC. We also showed that these regions respond differentially to positive and negative valence, most clearly in the medial frontal region where activation was more dorsal for negative stories and ventral for the positive condition. The findings of the present study also suggest that mentalizing alone does not account for the differences between emotional and neutral stories, as all of our stories required similar inferencing of the feelings of the protagonist. Finally, our results for the judgment task showed striatal and amygdala activations, whereas we failed to show similar activations for stories, suggesting the importance of decision making factors on emotional processes.

Chapter 4 - Emotional language processing in autism

Purpose

The overall goal of the study presented herein was to extend the paradigm used in Study 1 to include autistic individuals. Specifically, to determine a) whether individuals with autism are able to make emotional inferences in the language context, and b) to investigate the extent to which autistic individuals use the neural systems typically associated with language and/or social-affective processes when making these inferences as compared to typically achieving peers.

As described in detail in preceding chapters, social-emotional understandings require that one is able to both understand the message explicitly stated in spoken communications, as well as to draw inferences implicitly conveyed in others' verbalizations. These inferences often include information related to emotion, as in the negative feelings implied in, "When I went to my car this morning I saw there was a large dent in it." Such inferences—as they relate to others—also require social processes of mentalizing or theory of mind (ToM), or the ability to attribute mental states to others and use this information to explain or make predictions about them. Thus, making such inferences about others' *emotional* states requires processes associated with both mentalizing and language comprehension.

In autism, deficits have been shown in processes related to mentalizing (Frith & Frith, 1999; Frith & Frith, 2003; Frith, 2001) and to emotions (Begeer et al., 2008; Nuske et al., 2013). Findings regarding emotional language specifically in ASD are mixed, as discussed in detail in Chapter 2, although the evidence suggests that comprehension skills are generally stronger than expressive abilities. Thus, the main

question posed in this study is whether the process of making emotional inferences from spoken language in autism is associated with reduced neural activity in the brain regions typically linked to the ToM network, including medial prefrontal cortex (mPFC), posterior cingulate cortex (pCC), bilateral- anterior and posterior superior temporal sulci (aSTS, pSTS), and temporal parietal junction (see Mar, 2011 for review), those implicated in processing emotions, i.e., anterior cingulate cortex (aCC), medial- and ventromedial prefrontal cortex (mPFC, vmPFC), and amygdala (see Citron, 2012 for review), or whether autistic individuals engage compensatory neural activity in areas typically involved in inferential language processing, i.e., aSTS, pCC, dorsal medial prefrontal cortex (dmPFC), and inferior frontal gyrus (IFG), superior temporal gyrus (STG) bilaterally (see Ferstl & Neumann, 2008 for review).

To investigate this question, functional MRI data from adolescents and adults with autism was compared to typically developing peers on an Emotional Inference Task (EIT). This study replicates the one described in Chapter 3 in terms of stimuli and design, with improvements made to the scanning protocol (see Methods). Briefly, emotionally valent (positive or negative) and neutral (physical state) short stories were presented verbally in an event-related fMRI study, and subjects were asked to make a true-or-false (T/F) congruency judgment pertaining to the inference to be drawn. This experimental design allowed me to compare cortical responses to the scenario from which the emotional inference is drawn as well as from the congruity judgment in both neurotypical and autistic individuals. This is an improvement on previous behavioral- as well as existing imaging experiments concerning emotional

language processing in autism. For example, Catarino et al. (2011) presented written emotional (and concrete) sentences with congruent or incongruent final words. Their analysis focused solely on the decision-making component of the judgment, and therefore failed to determine whether the core deficit in emotional inferences for ASD was in the response to the event/context or the subsequent task component (congruity judgments or word selection). In addition, this study identified neural activity in response to both positive and negative valence separately (rather than collapsing the conditions of emotion) without the use of emotionally explicit language (Han et al., 2014; Mason et al., 2008). Finally, this study employed simultaneous accelerated multiband (MB) imaging (Moeller et al., 2010) in an interleaved echo planar imaging (EPI) pulse sequence which has been shown to result in a higher (temporal and spatial) resolution thus enabling more accurate measurement of functional responses (Feinberg & Stetsompop, 2013; Xu, Kemeny, Park, Frattali, & Braun, 2005). At the time of this writing, no reported studies have employed these methods in autism.

Hypotheses

Research shows that emotional deficits are one characteristic of autistic individuals (Chapter 2 and Begeer et al., 2008; Nuske et al., 2013). One hypothesis suggests that emotional deficits in autism are due to the inability to understand what others are thinking or feeling, that is, more generalized ToM deficits (Frith & Frith, 1999; Frith & Frith, 2003; Frith, 2001) occurring with abnormal functioning of associated brain regions: medial prefrontal cortex (mPFC), posterior cingulate cortex (pCC), bilateral- anterior and posterior superior temporal sulcus (aSTS, pSTS), and temporal parietal junction (TPJ; Frith & Frith, 2003; Gallagher & Frith, 2003; Mar,

2004; Saxe & Kanwisher, 2003; Saxe & Powell, 2006). In autism, aberrant brain activity in regions of the ToM network (mPFC, pCC, bpSTS, bTPJ) have been shown during mental state attribution tasks (Baron-Cohen et al., 1999; Castelli, 2005; Kana et al., 2009; Piggot et al., 2004), in narrative comprehension (Happe, Ehlers, Fletcher, & Frith, 1996; Mason et al., 2008) and specifically during emotional narratives (Mason et al., 2008). A second hypothesis is that emotional deficits are driven by a failure to elicit appropriate emotional responses to depicted events. Generation of an emotional response to stimuli can also be assessed in terms of brain activation. Individuals with autism often show reduced response (particularly in amygdala and prefrontal regions) to emotion in faces (Ashwin et al., 2007; Critchley et al., 2000; Dapretto et al., 2006; Piggot et al., 2004; Wang et al., 2004) and negatively valenced words (Kennedy et al., 2006), but few studies have looked at response to emotional inference from linguistic stimuli in autism (Catarino et al., 2011; Han et al., 2014; Mason et al., 2008). Neurotypical (NT) individuals activate several regions in response to emotionally valent linguistic stimuli including: the rostral anterior cingulate cortex (raCC; Whalen et al., 1998), orbitofrontal cortex (Hynes et al., 2006; Maratos, Dolan, Morris, Henson, & Rugg, 2001), and bilateral amygdala (Ferstl, Rinck, & Von Cramon, 2005; Isenberg et al., 1999; Kiehl et al., 2001; Strange, Henson, Friston, & Dolan, 2000). No study has yet examined whether these "social-affective" brain regions, that is, the ToM network and/or regions associated with emotion (mPFC, aCC and amygdala), show reduced activation in autism when another person's emotion must be inferred from story context.

Using fMRI in the design described above, neural activations were measured in response to both the emotional events described in the passages as well as the congruity judgment to the emotion word. Behavioral measures of response time and accuracy on the judgments were also collected. My primary hypotheses (Table 6, 7) were that autistic individuals would show adequate abilities in making congruency judgments but will fail to show typical cortical activations in social-affective brain areas to emotional story context (excepting the aCC, which may be recruited at it is implicated in both emotional processes and comprehending inferential language). According to this hypothesis, relative to NT individuals, autistic individuals would: 1) elicit little to no activity in areas associated with social-affective processes while listening to the stories describing an emotional event, 2) show more activation in response to the incongruent target items compared to the congruent condition. Specifically, activation will be seen in the cognitive control network including the dorsolateral prefrontal cortex (dlPFC) and posterior aCC (as opposed to rostral aCC) involved in error monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001). In terms of accuracy and response times, the autistic group should exhibit similar characteristics to the NT group (and to the pattern shown in Study 1): 1) correct identification of target, 2) faster and more accurate responses to emotional compared to neutral stories and 3) faster responses to congruent relative to incongruent targets (Ochsner, Hughes, Robertson, Cooper, & Gabrieli, 2009), but overall slower response times (Table 8). Another possibility is that individuals with ASD *do* elicit emotion to the described events but fail to link these responses to the appropriate labels (e.g., *happy*, *sad*). Accordingly, they will perform poorly on behavioral tasks requiring

these referents. According to this hypothesis, relative to NT individuals, individuals with ASD should: 1) elicit reduced activity in the social-affective areas of the brain while listening to the stories describing an emotional event, and 2) show less activation to incongruent items as they do not detect the incongruency between the verbal label for emotion and the sentence context in the cognitive control network (above). A third prospect is that it is the *label* of emotion that is problematic not the failure to elicit emotion, autistic individuals would elicit a response (activation) to the emotional passage in the social-affective regions, but still fail to detect the incongruity both behaviorally and cortically on the Target Sentence which is determined by the label of the emotion.

Table 6.

Primary hypotheses: neural response to scenarios, Study 2

	EMO			NEUT		
Regions	ASD		NT	ASD		NT
Theory of mind						
mPFC		<	✓			
pCC		<	✓			
baSTS		<	✓			
bpSTS		<	✓			
bTPJ		<	✓			
Emotion						
aCC	✓	=	✓			
mPFC		<	✓			
vmPFC		<	✓			
Amygdala		<	✓			
Inferential language						
dmPFC	✓	=	✓	✓	=	✓
aCC	✓	=	✓	✓	=	✓
baSTS	✓	=	✓	✓	=	✓
bIFG	✓	=	✓	✓	=	✓
bSTS/MTG	✓	=	✓	✓	=	✓

Note. Summary of predictions for brain areas associated with theory of mind, emotion and inferential language in response to emotional (EMO) and neutral (NEUT) scenarios for autism (ASD) and neurotypical (NT) groups.

Table 7.

Primary hypotheses: neural responses to judgments, Study 2

	Congruency					
	INCON > CON			CON > INCON		
Regions	ASD		NT	ASD		NT
aCC		<	✓			
dlPFC		<	✓			
Right IPL		<	✓			
Precuneus					<	✓
pCC					<	✓
Insula					<	✓

Note. Summary of predictions for brain areas associated with cognitive control. Abbreviations: aCC, anterior cingulate cortex; ASD, individuals with autism; CON, congruent; dlPFC, dorsolateral prefrontal cortex; INCON, incongruent; NT, neurotypical individuals; pCC, posterior cingulate cortex.

Table 8.

Primary hypotheses: behavioral results, Study 2

Measure	*Contrast*		
Response times			
Story valence	EMO	<	NEUT
Target	CON	<	INCON
Group	NT	<	ASD
Accuracy			
Story valence	EMO	=	NEUT
Target	CON	=	INCON
Group	NT	=	ASD

Note. Abbreviations: ASD, individuals with autism; CON, congruent; EMO, emotion; INCON, incongruent; NEUT, neutral; NT, = neurotypical individuals.

My primary hypothesis is that correct identification of depictions of socially-relevant emotional situations (in language) is associated with a failure to *elicit social-emotional responses* to affective stimuli. An alternative hypothesis is that autistic individuals will fail to elicit social-affective responses to emotional story contexts due to generalized language deficits or to more specific difficulties with engaging

emotion from linguistic context. It has been shown that individuals with autism have greater difficulty with drawing global inferences from language *in general* (Joliffe & Baron-Cohen, 2000; Losh & Caps, 2003). Additionally, neuroimaging studies find abnormalities in activation patterns during non-social or emotional language processing (review, see Groen et al., 2008). In this case, failure to infer the emotional consequences of the events described in a story would be due to this generalized language deficit. Thus, autistic individuals would have similar difficulties making emotional *and* non-emotional inferences and would perform poorly on the congruity judgment in the EIT for both items. The processing of both incongruent vs. congruent items would then fail to elicit activation in cognitive control networks in ASD for both emotional and neutral words.

Methods

Participants

Fifteen participants with autism (ASD; ages 16 - 29, 13 males) and 16 neurotypical controls (NT) (ages 16 - 29, 13 males) were recruited. Data from one participant in the autism group was excluded due to movement. Six of the 14 autistic participants were medicated when scanned: 5 received SSRIs, 3 CNS stimulants, 2 antipsychotic drugs and 3 other antidepressants (note that two of the medicated autistic participants were treated with more than one drug). One of the control participants was medicated with an antidepressant. Besides the ASD diagnosis in the autism group, all participants reported being free of auditory deficits, major medical conditions, and had no history of head trauma (loss of consciousness of more than ten

minutes and/or head injury). Participants received a thorough explanation of the experimental procedures, and written consent was obtained in accordance with the requirements of the Institutional Review Board of University of Maryland. Subjects received monetary compensation for participation.

Behavioral assessments

Full scale IQ was assessed with the Vocabulary and Matrix Design subtests of the Wechsler Abbreviated Scale of Intelligence (WASI) or Wechsler Adult Intelligence Scale (WAIS). Language ability was further assessed using the Sentence Memory (test 15) from the Wide Range Assessment of Memory and Learning (WRAML-2; Sheslow & Adams, 1990), a sentence repetition task shown to be closely related to general language ability in autism (Kenworthy et al., 2012), and the Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock et al., 2001). Diagnoses for participants in the autism group were confirmed with the Autism Diagnostic Observational Scales-Revised (ADOS-R; Lord et al., 2000), administered by a trained and research-reliable clinician, and ASD symptomatology was further assessed using two measures. The first, the Autism Quotient (AQ; Appendix F, Table 1; Baron-Cohen, Wheelwright, Skinner, et al., 2001), is a self-administered questionnaire designed to measure autistic symptoms in adults with normal intelligence. While not diagnostic, the scale was developed using diagnostic criteria. Scores range from 0-50, higher scores being indicative of more autistic symptoms. In a large pilot study, Baron-Cohen and colleagues (2001) showed that adults with autism had a mean AQ score of 35.8 (SD = 6.3), which was significantly higher than matched controls (M = 16.4, SD = 6.2). Furthermore, in the

control group but not in the autism group, men (*M* = 17.8, *SD* = 6.8) scored significantly higher than women (*M* = 15.4, *SD* = 5.7), and more males than females (40% versus 20%) scored in the intermediate range (20+ points). The AQ underscores the theory that autistic traits occur on a continuum in the ASDs and the neurotypical population, as similar processing styles are seen in those with high scores on the AQ and autistic individuals (Almeida, Dickinson, Maybery, Badcock, & Badcock, 2010; Clark, Hughes, Grube, & Stewart, 2013; Robertson & Simmons, 2013; Wainer, Ingersoll, & Hopwood, 2011). The second measure, the Social Communication Questionnaire (SCQ; Appendix F, Table 2; Rutter, Bailey, & Lord, 2003) is a list of yes/no questions focused on an individual's early development in terms of language use and social functioning. Out of a total possible 40 points, a score of 15 or higher is used to differentiate autism from other diagnoses. Two separate studies have demonstrated the questionnaire's internal consistency (.81-.93; Naglieri & Chambers, 2009).

Several additional self-report instruments were also included to evaluate characteristics and traits commonly associated with autism spectrum disorders. The first three are general measures of social- and emotional functioning. Firstly, participants completed the Empathy Quotient (EQ; Appendix F, Table 3; Baron-Cohen & Wheelwright, 2004), consisting of 40 empathy items and 20 fillers, with higher scores being associated with higher empathic abilities. In their pilot data, Baron-Cohen and colleagues (2004) show that, out of a total possible 80 points, adults with ASDs scored significantly lower (*M* = 20.4, *SD* = 11.6) than matched controls (*M* = 42.1, *SD* = 10.6). Additionally, these scores were inversely related with

their AQ scores (r = -0.56, p < .001). The second is designed to evaluate alexithymia, a condition characterized by reduced ability to interpret emotional states, both one's own as well as others. Several studies have suggested that the emotional impairments in autism are due to alexithymia, rather than this being a *feature* of autism, (Bird & Cook, 2013; Bird et al., 2010; Cook, Brewer, Shah, & Bird, 2013). The 20-Item Toronto Alexithymia Scale (TAS-20; Appendix F, Table 4; Bagby, Parker, & Taylor, 1994; Bagby, Taylor, & Parker, 1994; Parker, Taylor, & Bagby, 2003) results in scores from 1-100, and scores ≥ 61 are suggestive of high alexithymia, while those ≤ 51 = low symptomatology. Autistic individuals (M = 60.44, SD = 10.84) generally score higher than matched controls (M = 42.51, SD = 9.09) (Hill et al., 2004). Thirdly, to measure "mentalizing" abilities, the "Reading the Mind in the Eyes-Revised" (MinE; Appendix F, Table 5; Baron-Cohen, Wheelwright, Hill, et al., 2001) was employed. In this test, participants identify emotion conveyed in 40 black & white photographs of eye regions by matching one of four emotional words to the image. Out of the 40 possible points, pilot data shows autistic individuals make fewer accurate decisions (M = 21.9, SD = 6.6) compared to IQ matched controls (M = 30.9, SD = 3.0). Two more questionnaires were included, the first to evaluate overall "trait" anxiety levels (as compared to "state") because anxiety disorders are prevalent in autism (Gillott & Standen, 2007; Simonoff et al., 2008; van Steensel, Bögels, & Perrin, 2011). For this, the STAIT (Appendix F, Table 6; State-Trait Anxiety Inventory; Spielberger, 2010) was administered, a 20-item self-report assessment that has undergone various reliability and validity tests, providing evidence that it is an adequate measure for studying anxiety in research and clinical settings (Sesti, 2000).

Higher scores (on a scale of 1-80) suggest higher anxiety levels. The next questionnaire concerns levels of loneliness, also associated with autism disorders (Mazurek, 2013). The 20-item UCLA Loneliness Scale (version 3) is shown to be highly reliable, both in terms of internal consistency and test-retest reliability (UCLA; Appendix F, Table 7; Russell, 1996), and out of a possible 60 points, higher scores suggest higher degrees of loneliness. Finally, all participants completed the Edinburgh Handedness Inventory (Oldfield, 1971).

Group characteristics

Table 9 summarizes the demographic information and assessments the both groups. Notably, there are no group differences for age ($t(28) = -.95$, $p = .368$; ASD: $M = 26.36$, $SD = 13.7$; NT: $M = 20.63$, $SD = 12.2$), gender ($\chi^2 (1) = 0.11$, $p = .743$), full scale IQ ($t(28) = -1.90$, $p = .067$; ASD: $M = 116.8$, $SD = 13.8$; NT: $M = 126.2$, $SD = 13.2$), Matrix Reasoning IQ ($t(28) = -1.27$, $p = .214$; ASD: $M = 56.1$, $SD = 6.9$; NT: $M = 60.1$, $SD = 9.5$), or WJIII Oral Comprehension scores ($t(28) = -1.42$, $p = .809$; ASD: $M = 27.0$, $SD = 4.3$; NT: $M = 28.8$, $SD = 2.6$). However, between-group differences were revealed in the verbal IQ scores ($t(28) = -2.41$, $p = .023$; ASD: $M = 62.6$, $SD = 9.3$; NT: $M = 69.5$, $SD = 6.4$) and WRAML-2 ($t(28) = -2.27$, $p = .031$; ASD: $M = 10.07$, $SD = 3.0$; NT: $M = 12.4$, $SD = 2.5$) scores in this sample. Boxplot diagrams comparing the results of each of the behavioral assessments for both groups are found in Appendix E. In the measures designed to assess autistic characteristics, results are consistent with expectations, that is, the group with autism shows more autistic symptomatology than the controls. Specifically, the Autism Quotient (AQ; $t(28) = 4.41$, $p < .0001$) shows that the ASD group ($M = 28.5$, $SD = 8.2$) exhibit more

autistic traits compared to NT (*M* = 15.0, *SD* = 8.5), likewise the Social Communication Questionnaire (SCQ: $t(28) = 5.77$, $p < .0001$), suggests that the ASD group (*M* = 20.9, *SD* = 4.4) displayed more *early* autistic symptomatology compared to NT (*M* = 9.6, *SD* = 6.0). Additionally, the Empathy Quotient (EQ; $t(28) = -5.75$, $p < .0001$), suggests that the ASD group (*M* = 24.9, *SD* = 11.9) has impaired empathizing abilities compared to controls (*M* = 46.4, *SD* = 9.4), the Mind in the Eyes ($t(28) = -2.58$, $p = .015$), suggests that ASD group (*M* = 22.9, *SD* = 4.7) is less able to empathize via photos of eyes relative to controls (*M* = 27.06, *SD* = 4.3), and the Toronto Alexithymia Scales (TAS-20; $t(28) = 2.26$, $p = .032$), shows that autistic participants (*M* = 52.6, *SD* = 14.6) have impairments in identifying emotions compared to NT (*M* = 42.6, *SD* = 9.6). However, the same is not observed for either the anxiety scales (STAIT; $t(28) = 1.42$, $p = 1.66$), [ASD (*M* = 48.2, *SD* = 10.2); NT (*M* = 42.5, *SD* = 11.4)] or the loneliness assessment (UCLA; $t(28) = 1.21$, $p = .418$), where the groups' scores were equal [ASD (*M* = 26.36, *SD* = 13.7); NT (*M* = 20.63, *SD* = 12.2)]. In order to further investigate the nature of these metrics within each group and determine their relationship, within-group correlations were conducted. Results of these analyses are summarized in Tables 10 and 11 for the ASD group and the NT group respectively. In the autism group, measures of autistic characteristics covary, but not with language or IQ, suggesting that ASD symptomology is separate from cognitive and linguistic ability in this sample. Specifically, for cognitive measures, Full-Scale IQ scores are significantly correlated with Verbal IQ, r =.912, Matrix Reasoning IQ, r =.846, and oral comprehension abilities (WJIII), r =.765 (all *p*s < 0.01), but not sentence repetition (WRAML-2) scores. For Verbal IQ scores

however, we see a significant relationship between Matrix Reasoning IQ, r =.614, sentence repetition (WRAML-2), r =.656 and oral comprehension scores (WJIII), r =.722 (all ps < 0.05). For measures concerning autistic characteristics, Autism Quotient scores are significantly related to other social-emotional measures, specifically one's social communication development scores (SCQ), $r = .564$, $p < 0.5$, poor empathy abilities (EQ), $r = -.817$, $p < 0.01$, and impaired mentalizing abilities (Mind in the Eyes) $r = -.643$, $p < 0.5$. Further, there were also significant relationships between this group's mentalizing (Mind in Eyes) (in)abilities and their empathy ratings (EQ) $r = -.738$, $p < 0.01$, alexithymia (TAS-20) scores $r = -.746$, $p < 0.01$, levels of anxiety (STAIT) $r = -.583$, $p < 0.5$ and degree of loneliness (UCLA) $r = -.583$, $p < 0.5$.

Table 9.

Demographic and symptoms assessment information, Study 2

	ASD (n = 14)	NT (n = 16)	Statistics	*p*
Age (years)	21.26 ± 4.1	22.70 ± 4.5	*t*(28) = -.95	.368
(range)	(*16 – 29*)	(*16 – 29*)		
Gender (M/F)	12/2	13/3	χ^2 (1) = 0.11	.743
Full IQ	116.8 ± 13.8	126.2 ± 13.2	*t*(28) = -1.90	.067
(range)	(*89 – 133*)	(*88 – 140*)		
Verbal IQ	62.6 ± 9.3	69.5 ± 6.4	*t*(28) = -2.41	.023*
(range)	(*47 – 71*)	(*54 – 76*)		
Matrix Reasoning IQ	56.1 ± 6.9	60.1 ± 9.5	*t*(28) = -1.27	.214
(range)	(*40 – 61*)	(*29 – 68*)		
WRAML-2	10.07 ± 3.0	12.4 ± 2.5	*t*(28) = -2.27	.031*
(range)	(*3 – 15*)	(*7 – 17*)		
WJIII	27.0 ± 4.3	28.8 ± 2.6	*t*(28) = -1.42	.809
(range)	(*15 – 31*)	(*23 – 32*)		
AQ	28.5 ± 8.2	15.0 ± 8.5	*t*(28) = 4.41	< .001**
(range)	(*17 – 45*)	(*6 – 37*)		
SCQ	20.9 ± 4.4	9.6 ± 6.0	*t*(28) = 5.77	< .001**
(range)	(*13 – 28*)	(*3 – 23*)		
EQ	24.0 ± 11.9	46.4 ± 9.4	*t*(28) = -5.75	< .001**
(range)	(*3 – 37*)	(*33 – 60*)		
Mind in Eyes	22.9 ± 4.7	27.06 ± 4.3	*t*(28) = -2.58	.015*
(range)	(*15 – 29*)	(*17 – 33*)		
TAS-20	52.6 ± 14.6	42.6 ± 9.6	*t*(28) = 2.26	.032*
(range)	(*32 – 76*)	(*32 – 63*)		
STAIT	48.2 ± 10.2	42.5 ± 11.4	*t*(28) = 1.42	.166
(range)	(*31 – 69*)	(*23 – 60*)		
UCLA	26.36 ± 13.7	20.63 ± 12.2	*t*(28) = 1.21	.418
(range)	(*2 – 49*)	(*3 – 47*)		
ADOS-R total	9.64 ± 3.0	-		
ADOS-R communication	3.21 ± 1.4	-		
ADOS-R social	7.07 ± 2.2	-		
Manual preference	54.6 ± 67	78.0 ± 34	*t*(28) = -1.2	.229

Note. Data represent average scores ± standard deviation. IQ scores from the Wechsler Abbreviated Intelligence Scales (WASI) or Wechsler Adult Intelligence Scales (WAIS). WRAML-2: Wide Range Assessment of Memory and Learning scaled (age-adjusted) scores (Rutter, Bailey & Lord, 2003). WJIII: Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock et al., 2001). AQ: Autism Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). SCQ: Social Communication Questionnaire (Rutter, Bailey, & Lord, 2003). EQ: Empathy Quotient (Baron-Cohen & Wheelwright, 2004). Mind in Eyes: Reading the Mind in the Eyes-Revised (Baron-Cohen, Wheelwright, Hill, et al., 2001). TAS-20: Toronto Alexithymia Scales (Bagby, Parker, et al., 1994; Bagby, Taylor, et al., 1994). STAI: State Trait Anxiety Inventory (Spielberger, 2010). UCLA: UCLA Loneliness Questionnaire (Russell, 1996). ADOS-R: Autism Diagnostic Interview-Revised (Lord et al., 2000). Manual preference is reported as the Edinburgh score (from -100 completely left-handed to +100 completely right-handed).
**p* < 0.05, ***p* < 0.001

Table 10.

Demographic and systems assessment information for autism group, Study 2: Correlations and Descriptive Statistics

Variable	1	2	3	4	5	6	7	8	9	10	11	12
1. Full IQ	-											
2. Verbal IQ	.912**	-										
3. Matrix IQ	.846**	.614*	-									
4. WRAML2	.531	.656*	.456	-								
5. WJIII	.765**	.722*	.722**	.766**	-							
6. AQ	.148	.230	.097	.245	.171	-						
7. SCQ	-.105	-.026	-.237	-.273	-.172	.564*	-					
8. EQ	.195	.094	.225	-.090	.047	-.817**	-.611*	-				
9. Eyes	.406	.256	.442	.219	.267	-.643*	-.729**	-.738**	-			
10. TAS-20	-.452	-.400	-.355	-.136	-.321	.515	.368	-.563*	-.746**	-		
11. STAI	-.238	-.008	-.341	.204	-.052	.278	.142	-.414	-.583*	.553*	-	
12. UCLA	-.265	-.074	-.261	.250	.108	.268	.166	-.510	-.583*	.498	.762**	-
M	116.79	62.57	56.14	10.17	27.00	28.5	20.86	24.00	22.86	52.64	48.21	26.36
SD	13.80	9.29	6.90	3.02	4.31	8.24	4.36	11.88	4.67	14.56	10.21	13.68
Range	89 - 133	47 - 71	40 - 61	3 - 15	15 - 31	17 - 45	13 - 28	3 - 37	15 - 29	32 - 76	31 - 69	2 - 49

Note. N = 14. 1-3. Full-, Verbal- and Matrix Reasoning IQ scores from the Wechsler Abbreviated Intelligence Scales (WASI) or Wechsler Adult Intelligence Scales (WAIS), Verbal- and Matrix IQ scores = *t*-scores. 4. WRAML2, Wide Range Assessment of Memory and Learning age-adjusted scaled scores (Rutter, Bailey & Lord, 2003). 5. WJIII, Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock et al., 2001). 6. AQ, Autism Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). 7. SCQ, Social Communication Questionnaire (Rutter, Bailey, & Lord, 2003). 8. EQ, Empathy Quotient (Baron-Cohen & Wheelwright, 2004). 9. Eyes, Reading the Mind in the Eyes-Revised (Baron-Cohen, Wheelwright, Hill, et al., 2001). 10. TAS-20, Toronto Alexithymia Scales (Bagby, Parker, et al., 1994; Bagby, Taylor, et al., 1994). 11. STAI, State Trait Anxiety Inventory (Spielberger, 2010). 12. UCLA, UCLA Loneliness Questionnaire (Russell, 1996).

*$p < 0.05$, **$p < 0.01$

Table 11.

Demographic and systems assessment information for neurotypical group, Study 2: Correlations and Descriptive Statistics

Variable	1	2	3	4	5	6	7	8	9	10	11	12
1. Full IQ	-											
2. Verbal IQ	.869**	-										
3. Matrix IQ	.880**	.621*	-									
4. WRAML2	.569*	.595*	.480	-								
5. WJIII	.701**	.664*	.673**	.440	-							
6. AQ	-.463	-.284	-.608*	-.197	-.283	-						
7. SCQ	-.562*	-.496	-.554*	-.512*	-.484	.727**	-					
8. EQ	.585*	.539*	.390	-.506*	.542*	-.382	-.664**	-				
9. Eyes	.767**	.615*	.781**	.668**	.644**	-.527*	-.531*	-.542*	-			
10. TAS-20	-.576*	-.392	-.676**	-.132	-.783**	.456	.596*	-.533*	-.502*	-		
11. STAI	-.323	-.102	-.321	-.163	-.336	.342	.244	-.484	-.163	.435	-	
12. UCLA	-.153	-.077	-.324	-.146	.302	.125	.108	-.331	-.224	.490	.520*	-
M	126.19	69.5	60.0	12.38	28.81	15.00	9.63	46.38	27.06	42.56	42.56	20.63
SD	13.25	6.39	9.54	2.53	2.59	8.45	6.02	9.42	4.25	9.64	11.38	12.21
Range	88 – 140	54 – 76	29 – 68	7 – 17	23 – 32	6 – 37	3 – 23	33 – 60	17 – 33	32 – 63	23 - 60	3 - 47

Note. N = 16. 1-3. Full-, Verbal- and Matrix Reasoning IQ scores from the Wechsler Abbreviated Intelligence Scales (WASI) or Wechsler Adult Intelligence Scales (WAIS), Verbal- and Matrix IQ scores = *t*-scores. 4. WRAML2, Wide Range Assessment of Memory and Learning age-adjusted scaled scores (Rutter, Bailey & Lord, 2003). 5. WJIII, Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock et al., 2001). 6. AQ, Autism Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). 7. SCQ, Social Communication Questionnaire (Rutter, Bailey, & Lord, 2003). 8. EQ, Empathy Quotient (Baron-Cohen & Wheelwright, 2004). 9. Eyes, Reading the Mind in the Eyes-Revised (Baron-Cohen, Wheelwright, Hill, et al., 2001). 10. TAS-20, Toronto Alexithymia Scales (Bagby, Parker, et al., 1994; Bagby, Taylor, et al., 1994). 11. STAI, State Trait Anxiety Inventory (Spielberger, 2010). 12. UCLA, UCLA Loneliness Questionnaire (Russell, 1996).
*$p < 0.05$, **$p < 0.01$

The pattern observed in the neurotypical group is dissimilar to that of the autism group. That is, IQ and language scores show significant relationships both to one another and to several of the social-affective measures. For cognitive/language measures, Full scale IQ was significantly correlated with Verbal IQ, $r = .869$, Matrix Reasoning IQ, $r = .880$, oral comprehension scores (WJIII), $r = .701$ (all ps < 0.01), and sentence repetition abilities $r = .569$, $p < 0.5$. Further, IQ correlated significantly with all autism measures except AQ scores, specifically, higher IQ scores were related to better social communication development ratings (SCQ), $r = -.562$, $p < 0.5$, empathetic abilities (EQ), $r = .585$, $p < 0.5$, ability to understand emotions from eyes (Mind in Eyes), $r = .767$, $p < 0.01$, and low alexithymia scores (TAS-20), $r = -.576$, $p < 0.5$. For non-cognitive measures, social and communication development (SCQ) scores covaried with several scales, including the autism quotient (AQ), $r = .727$, $p < 0.01$, ability to empathize, $r = -.664$, $p < 0.01$, intact mentalizing (Mind in Eyes), $r = -.531$, $p < 0.05$, and low levels of alexithymia (TAS-20), $r = .596$, $p < 0.05$. Unlike the autism group, in the neurotypical sample, AQ ratings bore a significant relationship to only social and communication development (SCQ) scores, $r = .727$, $p < 0.01$, and mentalizing abilities (Mind in Eyes), $r = -.527$, $p < 0.05$.

Task Procedures

See Chapter 3.

Acquisition of functional MR data

Subjects were scanned using a Siemens 3T Trio MRI system with a 32-channel head coil. After a scout image was obtained and automated shimming

procedures performed, two high-resolution scans covering the whole brain were obtained to facilitate spatial normalization and positioning of subsequent scans. First, a 3D T1-weighted, magnetization-prepared rapid acquisition gradient echo (MPRAGE) scan (repetition time=2530 msec, echo time 1=2.15 msec, echo time 2=4.03 msec, echo time 3=5.91 msec, echo time 4=7.79; flip angle=7°, bandwidth=651 Hz/pixel, echo spacing=1.6 msec, field of view=230 mm, 176 sagittal slices; thickness=0.9 mm; 0.9 × 1.0 matrix); and second, a 3D T2-weighted scan matched to the T1 (repetition time=3200 msec, echo time=483 msec, variable flip angle, bandwidth=751 Hz/pixel, echo spacing=3.32 msec, Turbo Factor=145, field of view=230 mm, 224 sagittal slices; thickness=0.9 mm; 0.9 x 1.0 matrix). Functional images to estimate task-related activity were obtained with simultaneous accelerated multiband (MB) imaging in an interleaved EPI pulse sequence (repetition time=1000 msec, echo time=31 msec, multiband acceleration factor=6, 64 × 64 matrix, flip angle 90°, FOV 210 mm). Whole brain coverage was obtained with 66 transversal slices (thickness=2.2 mm; in-plane resolution=2.2 × 2.2 mm).

Data Analysis

Analysis of behavioral data

Performance measures were accuracy and response time (calculated on correct trials only) to the 3sec EIT Target sentence epoch during fMRI acquisition. Group effects were calculated for accuracy and response time separately with repeated measures analysis of variance (ANOVA), using between-subject factor of group (ASD versus NT), and with-in subjects factors of 2 (congruent, incongruent) by 3 (positive, negative, neutral). Within group effects were calculated using 2 (congruent,

incongruent) by 3 (positive, negative, neutral) repeated measures ANOVAs for each group. Post-hoc pairwise comparisons were Bonferroni corrected. Statistical analyses of behavioral data were performed using IBM SPSS (version 23.0).

Functional MRI data preprocessing and statistical analysis

Data analysis was performed using Statistical Parametric Mapping (SPM12, http://www.fil.ion.ucl.ac.uk/spm). Preprocessing of the EPI time series included: (1) realignment for head motion correction, (2) spatial normalization into the Montreal Neurological Institute (MNI) anatomical space, and (3) spatial smoothing (5mm FWHM). Data were high pass filtered at 128 Hz, and examined for excessive motion and spiking artifacts using the Artifact Detection Tool (ART) software package. Outliers in the image time series (Z-threshold: 3.0, scan to scan movement threshold 1.0 mm were identified and excluded from subsequent statistical analysis (5.0% of the data). A functional run with > 20% outlier time points was excluded from the analysis, and individuals with more than one run with 20% outliers were excluded from the analyses. One functional run (of 4) from each of three of the autistic participants was not included in the analyses, one due to excessive motion, one due to participant's inability to hear, and one was not collected due to time constraints. One run from four control participants was excluded, two for low accuracy, one due to motion artifacts, and one was corrupted. For the remaining data, there were no significant differences in the number of outliers between groups, either across all four runs $t(28) = .820$, $p = .419$ or at the individual run level: run 1 $t(26) = -.646$, $p = .524$, run 2 $t(26) = .815$, $p = .422$, run 3 $t(227) = .521$, $p = .607$ run 4 $t(16.94) = 1.05$, $p = .309$.

First level analyses were conducted separately for the story and target response (probe). In the story model, each participant's design matrix contained the five stimulus conditions, three story factors: positive ("POS"), negative ("NEG"), and neutral ("NEUT") as well as the two probe conditions, congruent ("CON") and incongruent ("INCON"). The probe model contained seven conditions, the congruent and incongruent response to each level of valence ("PosCon," "PosIncon," "NegCon," "NegIncon," "NeutCon," and "NeutIncon") as well as one factor for the stories. In both models, all factors were convolved with a canonical hemodynamic response function (Friston et al., 1995). Six realignment parameters as well as outlier time points were included in the models as regressors of no interest. Each stimulus condition was compared with the implicit baseline condition to generate first-level contrast images (five per subject for story model, six for the probe model). Group results were obtained using random-effects analyses by combining subject-specific summary statistics across the group as implemented in SPM12.

For the stories, for each group, weighted contrasts combining the contrasts of all scenarios (POS+NEG+NEUT), the combined emotional (EMO) conditions (POS+NEG), and each condition separately POS, NEG and NEUT relative to the implicit baseline were computed. Despite having no specific predictions for autism regarding POS and NEG valence, these were included on an exploratory basis, and because results from Study 1 (neurotypical individuals) revealed clear differences between the conditions. A second set of between-group contrasts were computed to investigate the effects of the combination of contrasts of each story condition. *T*-contrasts from first level analyses were used to compare group effects within the

regions showing activity related the different conditions. A cluster corrected threshold of $p < .001$ was used. Results for contrasting conditions of valence, e.g., EMO > NEUT and NEUT > EMO, were also calculated, but unlike Study 1 (Chapter 2), these contrasts yielded few significant between-group activations and are therefore not reported herein.

For the response epoch, a two (group) x six (condition) ANOVA was performed for the three-second time window during which participants made congruency judgments. The main contrasts of interest were congruent and incongruent items separately, as well as the group * condition interactions. A cluster corrected threshold (FWE $p < .05$) was used on voxels surviving an initial threshold of $p < .001$.

Region of interest analyses

In order to further examine the putative systems underlying the neural activations to scenarios in greater detail, region of interest (ROI) analyses were conducted on the effects of interest for networks related to theory of mind- (TOM) and narrative (NARR) comprehension (See Chapter 3 for network definitions). (Separate ROI for emotion were not tested, as the main interest herein is the type of emotion processing consistent with making inferences about others' emotional states, as such it is expected to overlap with regions associated with mentalizing and language comprehension.) ROI were created from the results of an ALE meta-analysis, thus reducing Type I errors dramatically (Poldrack, 2007). ROI using data from Study 1 were not used as one goal of the present research is to disentangle neural activations related to ToM from those associated with language, and the

present stimuli (used in both studies) involves both processes. Importantly, Mar's (2011) narrative analysis included no ToM-related stories, and results for both story-related and nonstory-related ToM were reported separately. In order to identify the ToM network that is most like the stimuli in the present study, only the results for the ToM story (hereafter referred to as 'TOM' in the context of ROI analyses, and 'ToM' for theory of mind in general) were used. Regions of interest were generated by extracting significant clusters of activity for both TOM and NARR, as well as the conjunction of the two (TOM ∩ NARR) (MarsBaR; Brett, Anton, Valabregue, & Poline, 2002). Table 12 provides coordinate details and extent of the three ROI maps, Figure 8 illustrates the same. Regions of interest comprised voxels showing significant activation centered on the coordinate with peak intensity for that region for each of the contrasts of interest (2-sample *t*-tests for ASD, NT, ASD > NT, NT > ASD; EMO, NEG, POS, and NEUT). For these analyses, a threshold of $p < .002$, $k = 10$ was used (Lieberman & Cunningham, 2009). Percent signal change values were then extracted from 1-sample t-tests (FWE $p < .05$) for each ROI yielding significant activation.

Region of interest statistical analyses

In order to determine whether or not task-related neural activations were more or less predominant in language or mentalizing regions, three separate repeated measures ANOVA were run, one for each of the networks above (TOM, NARR, and TOM ∩ NARR), with condition (POS, NEG, NEUT) as the within-group measure and group (ASD, NT). Individual conditions and their parameter estimates for each ROI were nested within each group. Repeated measures ANOVAs were investigate

group x valence interactions in each ROI. Univariate ANOVAs were used to examine the effect of valence within each group, with parameter estimates for each ROI as the dependent variable, and valence as the fixed variable.

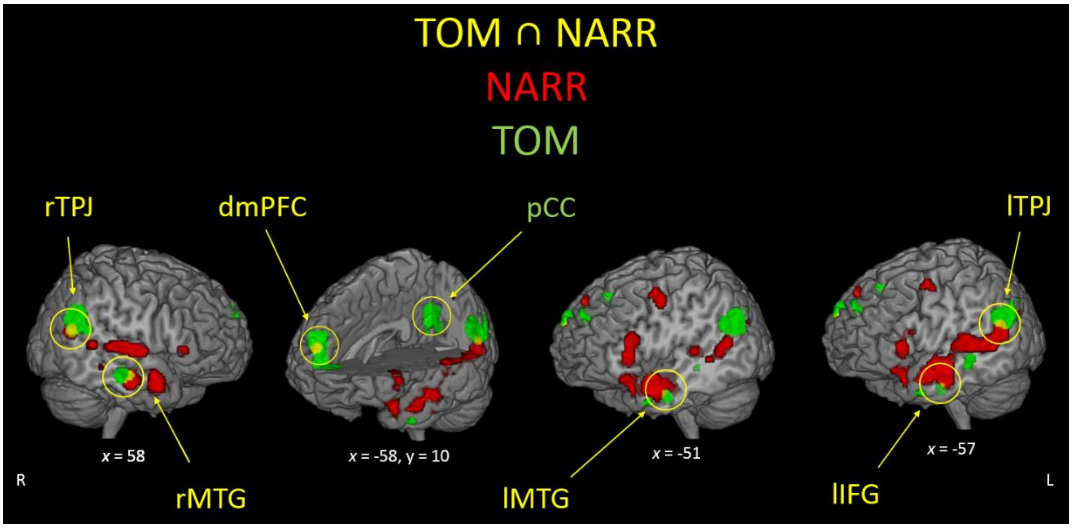


Figure 8. Maps for ROI analyses. Narrative comprehension (NARR, red) story-based theory of mind (TOM, green; Mar, 2011) and conjunction of the two (TOM ∩ NARR, yellow). Labels correspond to regions in TOM ∩ NARR. See Table 12 for details. Coordinates in MNI (Montreal Neurological Institute) space.

Table 12.

Labels and coordinates for regions of interest (ROI), Study 2

Region label	Lat	Number of voxels	MNI coordinates (maximum foci) *x*	*y*	*z*
TOM					
mPFC	-	7624	-1	54	31
TPJ	L	4072	-51	-59	27
TPJ	R	3696	54	-53	24
Precuneus	-	3392	-2	-55	29
IFG	R	1552	56	-17	-18
dmPFC	L	496	-18	54	31
sFG	L	336	-21	-3	-22
STS	L	328	-56	-29	-9
aCC	R	312	13	28	25
IFG	L	288	-52	-4	-30
Amygdala	L	168	-26	-3	-22
MOcc	R	152	-43	-71	35
aSTS	L	120	-52	12	-34
NARR					
STS	L	18288	-53	-12	-9
aSTS	R	3256	50	11	-27
IFG (triangularis)	L	2792	-50	26	10
STS	R	2728	57	-13	1
Precentral gyrus	L	1568	-45	1	49
mPFC	-	952	-1	59	23
MTG	R	840	56	-8	-24
TPJ	R	696	59	-58	15
dmPFC	-	328	-9	51	45
IFG (triangularis)	R	320	58	33	-1
IFG	L	312	-43	-17	-34
pSTS	R	288	55	-41	4
MTG	R	112	53	-33	-12
Parahippocampus	L	112	-19	-21	-14
IFG (opercularis)	L	80	-44	11	22
TPJ	L	64	-47	-67	18
TOM ∩ NARR					
dmPFC	-	469	3	59	23
TPJ	R	400	59	-57	16
	L	208	-55	-55	21
MTG	R	112	56	-10	-21
	L	32	-51	-2	-26
IFG	L	8	-54	-6	-28

Note. Table presents results for clusters from the theory of mind (TOM) story and narrative (NARR) comprehension meta-analyses (Mar et al., 2011) as well as the conjunction of the two (TOM ∩ NARR) used as basis for region of interest (ROI) analyses. Laterality right (R), left (L) or medial (‘-’). MNI, Montreal Neurological Institute.

Exploratory brain-behavior analyses

To examine whether neural activation was associated with cognitive and social-affective abilities as expressed in the behavioral assessments, exploratory correlation analyses were conducted for TOM ROI yielding task-related activity in POS, NEG and NEUT comparisons for each group separately. The reason for choosing TOM ROI—and for testing groups individually—is because research shows anomalous brain activity in regions of the ToM network (mPFC, pCC, bpSTS, bTPJ) in autism during mental state attribution tasks (Baron-Cohen et al., 1999; Castelli et al., 2005; Kana et al., 2009; Piggot et al., 2004) narrative comprehension (Happe et al., 1996; Mason et al., 2008), and specifically during emotional narratives (Mason et al., 2008). The individual valence contrasts (POS, NEG and NEUT) were chosen rather than the combined EMO condition in order to probe possible differences between conditions of valence. For social-affective processing, behavioral variables included AQ, EQ, SCQ, TAS-20, ADOS scores (Communication, Social, and Combined), and Reading the Mind in the Eyes. Cognitive and language measures were also tested, including IQ (Full Scale), WRAML, and WJIII.

Results

Behavioral Results

Accuracy

Between-group. For accuracy, a 2 (group) x 2 (congruency) x 3 (valence) repeated measures (RM) ANOVA showed a main effect of congruency ($F(1,28) = 11.13$, $p = .002$); responses to CON trials were more accurate than INCON. No other main effects were shown. Contrasts revealed a significant interaction of valence x

congruency between POS and NEUT, $F(1,28) = 6.20$, $p = .019$. Contrasts revealed that accuracy responses to CON were higher than for INCON in both condition. There was also a significant group x valence x congruency interaction between POS and NEUT, $F(1,28) = 4.90$, $p = .035$. Here, in the ASD group, responses to PosCon were less accurate than PosIncon, but NeutCon were more accurate than NeutIncon. However, in the NTs, accuracy was greater in the CON condition compared with INCON in both POS and NEUT.

Within-group. Repeated measures ANOVAs [2 (congruency) x 3 (valence)] for ASD showed a main effect for congruency, $F(1,28) = 4.90$, $p = .035$ such that CON trials ($M = 95.82$, $SE = 2.20$) received higher accuracy than INCON ($M = 90.80$, $SE = 3.42$). No significant effects were shown for NT.

Response time

Between-group. Statistical tests for RTs were conducted on correct trials only (5.46% of the trials removed). A 2 (group) x 2 (congruency) x 3 (valence) RM ANOVA showed a main effect of valence $F(2,56) = 29.66$, $p < .001$. Contrasts revealed that responses to both POS, $F(1,28) = 56.60$, $p < .001$, and NEG, $F(1,28) = 6.622$, $p < .016$, were significantly faster than for NEUT. There was also a main effect for congruency $F(1,28) = 21.63$, $p < .001$, where CON trial were faster than INCON $F(1,28) = 21.67$, $p < .001$. There was also a significant main effect of congruency on valence $F(2,56) = 7.06$, $p = .002$. Contrasts revealed that the difference between PosCon and PosIncon were significantly smaller than between NeutCon and NeutIncon, $F(1,28) = 18.44$, $p < .001$, and the same effect was seen between NegCon vs. NegIncon and NeutCon vs. NeutIncon, $F(1,28) = 5.670$, $p = .024$.

Within-group. For accuracy in the ASD group, there was a significant main effect of congruency, $F(1,13) = 15.78$, $p = .002$, as well as for valence $F(2,26) = 19.78$, $p < .001$. Contrasts reveals that POS was more accurate than NEUT, $F(1,13) = 30.81$, $p < .001$. In the NT group, a main effect was revealed for congruency $F(1.34,20.10) = 11.73$, $p < .001$, and valence, $F(1,15) = 5.52$, $p = .033$. Contrasts revealed that POS responses were faster than NEUT, $F(1,15) = 25.51$, $p < .001$. A significant interaction was shown for congruency on valence, $F(2,30) = 8.512$, $p = .001$, where responses to POS, $F(1,15) = 13.61$, $p = .002$, and NEG, $F(1,15) = 11.70$, $p = .004$, were faster than for NEUT (Figure 9 and Table 13, 14; Appendix G).

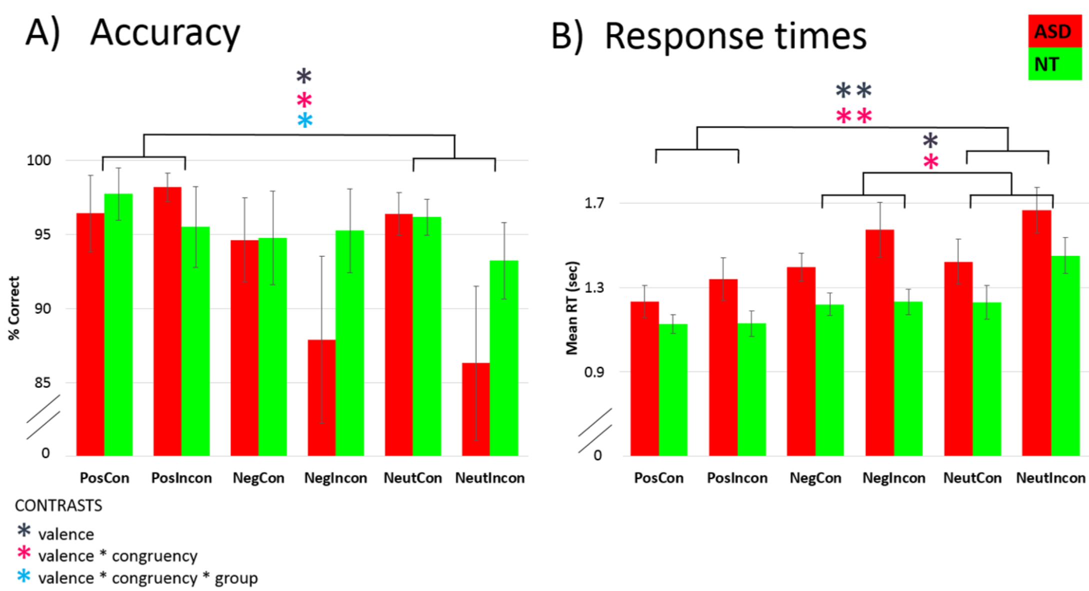


Figure 9. Behavioral effects for autism (ASD, red, $n = 14$) and neurotypical (NT, green, $n = 16$) for A: accuracy (% correct, T/F judgments) and B: response times (time from appearance of probe to button press.
Error bars: 95% CI.
*$p < .05$ **$p < .001$

Table 13.

Between-group behavioral effects, Study 2

	df	ACC *F*	ACC *p*	RT *F*	RT *p*
Valence	(2,56)	3.14	.051	29.66	.001**
Congruency	(1,28)	11.13	.002*	21.63	.001**
Valence * group	(2,56)	.94	.396	1.33	.274
Congruency * group	(1,28)	3.10	.090	3.13	.088
Valence * congruency	(2,56)	2.82	.068	7.06	.002*
Valence * congruency * group	(2,56)	2.99	.058	1.03	.365

Note. Effects of accuracy (ACC) and response time (RT): 2x2x3 repeated measures analysis of variance (ANOVA) with between-group factor (ASD, NT), and within-group factors: valence (POS, NEG, NEUT) and congruency (CON, INCON) for both accuracy and response time (RT) for autism (ASD) and neurotypicals (NT).
**p* < .05, ***p* < .001

Table 14.

Within-group behavioral effects, Study 2

	ASD df	ASD *F*	ASD *p*	NT df	NT *F*	NT *p*
ACC						
Valence	(2,26)	3.037	.065	(2,30)	.41	.666
Congruency	(1,28)	8.307	.013*	(1,15)	2.23	.156
Valence * congruency	(2,26)	3.320	.052	(2,30)	.906	.415
RT						
Valence	(2,26)	19.78	.001**	(1.34,20.10)	11.73	.001*
Congruency	(1,13)	15.78	.002*	(1,15)	5.52	.033*
Valence * congruency	(2,26)	3.32	.052	(2,30)	8.51	.011*

Note. Results for 2x3 repeated measures analysis of variance (ANOVA) with two factors: valence (POS, NEG, NEUT) and congruency (CON, INCON) for both accuracy and response time (RT) for autism (ASD) and neurotypicals (NT).
**p* < .05, ***p* < .001

Functional MRI Results

Scenarios

In order to verify that the task successfully engaged similar brain regions in both groups, whole brain analyses were calculated on all the scenarios (POS+NEG+NEUT) minus the implicit baseline. Within-group contrasts showed that

both the autistic group and the controls recruited extensive areas of activation in bilateral temporal lobes (with ASD extending further dorsally to include TPJ, especially on the RH), precentral/postcentral gyri, left inferior temporal gyrus, and cerebellum. The autism group had additional medial frontal activations, in both dmPFC and vmPFC. Significant clusters in between-group tests were found only in the ASD > NT contrast, in precuneus and paracentral lobule (and right SMA), bilateral IFG, and right middle frontal gyrus. Details of these results are found in Appendix H, Table 1, and Figure 1.

Emotional scenarios

ASD. Turning to the main results, within-group tests revealed that the ASD group showed strong task-related activity in response to the EMO conditions in a large number of brain regions involved in language processing, mentalizing and emotion, bearing in mind that there is a good deal of structural and functional overlap within these networks, for example in temporal lobes bilaterally (Figure 10 and Appendix H, Table 2). Regions characteristically identified with language inferencing (Ferstl & Neumann, 2008) included dorsal medial prefrontal cortex (dmPFC) [(-10, 50, 28), t=5.36], left inferior frontal gyrus (lIFG) [(-46, 22, 20), t=5.07] and large extents of significant activity encompassing left superior temporal sulcus and left middle temporal gyrus (lSTS, lMTG) [(-44, -26, 12), t=9.29; (-62, -14, -4), t=7.50]. On the right, activations were in STS/Heschl's gyrus [(50, -14, 6), t=9.89], and extended dorsally to include TPJ (see below). For regions typically identified with ToM (Mar, 2011), the autism group showed activity in right posterior temporal sulcus (rpSTS) [(54, -26, 10), t=7.79] and posterior cingulate cortex (pCC)/precuneus [(0, -

52, 30), t=5.27]. Regions involved with emotion included ventral medial prefrontal cortex (vmPFC) [(0, 52, -12), t=6.28] and amygdala [(-30, -2, 22), t=3.84] and medial prefrontal cortex (mPFC) [(-8, 60, 18), t=3.65], the latter being implicated in both ToM and emotional processing.

NT. Like the autism group, the neurotypical controls recruited areas more traditionally associated with language processing. In detail, task-related activations were found in dmPFC [(-2, 36, -24), t=5.21], and left IFG (-54, 24, 10), t=5.43], STS [(-54, -22, 0), t=8.72] and MTG [(-62, -32, 6), t=8.49]. Rightward temporal activity encompassed STS, MTG and anterior STS (aSTS) [(62, -16, -2), t=9.02; (62, 2, -16), t=8.90; (54, 8, -20), t=7.54]. In contrast with ASD, areas more commonly associated with mentalizing and/or emotion were not significantly engaged.

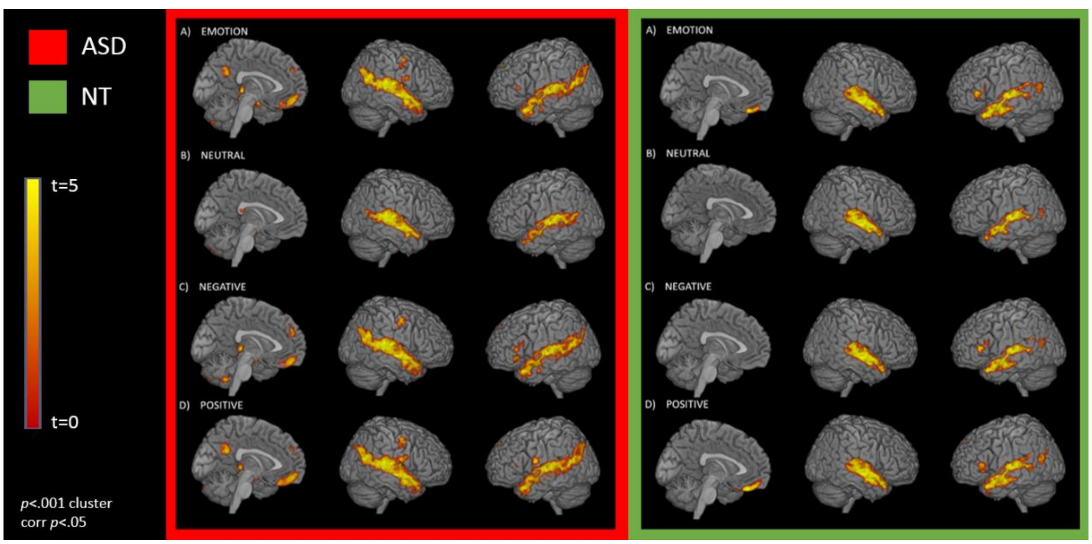


Figure 10. Within-group neural activations, Study 2. (A) Contrast of emotion (A), neutral (B), negative (C) and positive (D) scenarios in autism (ASD; red), neurotypical (NT; green). Task-related activity is displayed using a cluster corrected threshold of $p < .001$.

Between-group. The comparison of ASD > NT revealed activity in precuneus [(8, -54, 38), t=5.33], which is implicated in ToM (Mar, 2011). No regions showed

significantly greater activity for the neurotypical controls compared to the autism group for emotional scenarios.

Negative scenarios

ASD. In order to investigate whether or not the effect of valence had a differential contribution to those activations associated with emotional scenarios, within- and between-group tests were calculated for POS and NEG stories (Figures 10 and 11, and Appendix H, Table 3). In ASD, both conditions recruited similar brain regions, except that dmPFC and two clusters in lIFG were associated only with NEG. Furthermore, like the emotional condition most activity was observed in language-related brain areas for NEG, with the largest clusters of activation found in the temporal lobes. In the left hemisphere, the focal point of activity was centered in STG [(-50, -24, 6), t=11.21] and extended to MTG [(-62, -14, -4), t=8.78] and to TPJ. On the right, activity was focused in STS [(66, -26, 10), t=8.86]. As well, significant activations were found in lIFG (tri) [(-44, 26, 12), t=4.73], dmPFC [(10, 48, 24), t=5.79], and lIFG (orb) [(-52, 28, -4), t=5.38]. For areas typically associated with ToM, the precuneus [(6, -56, 36), t=5.16] was significantly engaged, and emotion-related regions included vmPFC [(2, 48, -20), t=5.93] and amygdala [(32, 0, -16), t=4.56].

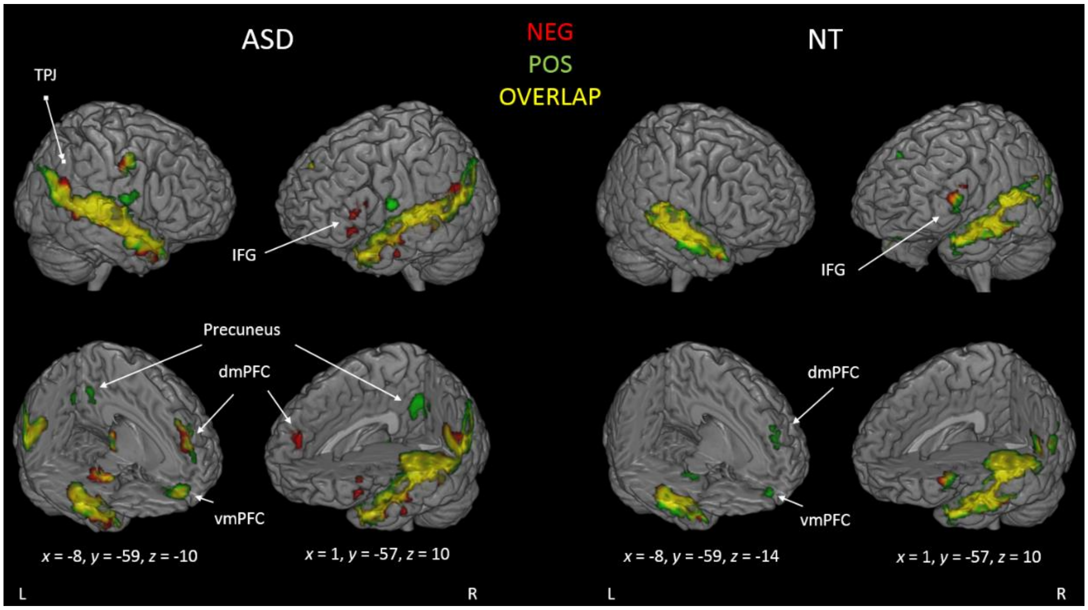


Figure 11. Within-group valence-related activity, Study 2. (A) Contrast of negative (NEG; red) and positive (POS; green) scenarios, overlap yellow. Autism group (ASD) on left; neurotypical controls (NT) on right. Task-related activity is displayed using a cluster corrected threshold of $p < .001$.

NT. Task-related activity for NEG in NT was found only in regions commonly associated with language processing. Specifically, the largest clusters of activity were in the temporal lobes. On the left, the strongest activation was in MTG [(-54, -22, 0), t=9.60] and extending to lSTG [(-62, -20, 6), t=9.14], and a smaller cluster in lIFG (tri) [NT (-54, 24, 10), t=5.04]. On the right, activity was focused in STS [(62, -16, -2), t=9.52] and including rMTG, [(62, 2, -16), 7.47].

Between-group. Like EMO, the direct comparison of ASD > NT revealed a significant cluster in precuneus [(6, -56, 36), t=5.17]. NT > ASD activations failed to reach significance.

Positive scenarios

ASD. Similar to negative, the POS stories were associated with language-related activity, and in the ASD group areas associated with mentalizing and emotion

were also engaged. For the former, temporal lobes showed large areas of left hemisphere (LH) activation in STG [(-50, -24, 6), t=11.88], MTG [(-62, -42, 4), t=8.30] and IFG (tri) [(-46, 22, 20), t=4.98] and in the right hemisphere (RH) STG [(58, -16, 0), t=9.55]. A cluster in dmPFC was also significantly involved [(-8, 50, 28), t=5.52]. For ToM-related areas, precuneus/PCC was significantly activated (for POS but *not* for NEG) [(-4, -50, 26), t=5.44], and for regions linked to emotion, a cluster in vmPFC was significant [(0, 54, -12), t=5.71].

NT. For the neurotypical controls, the most noticeable results was in the medial frontal lobe, where both ventral- [(-2, 34, -24), t=6.18] and dorsal mPFC (as well as small parahippocampal cluster) were activated for POS scenarios, but not NEG. Beyond this, activity was similar to that seen in the POS condition for NT. Specifically, temporal activations included lSTG [(-50, -24, 4), t=10.35], lMTG [(-62, -32, 8), t=9.16] and lIFG (tri) [(-54, 24, 10), t=5.57], as well as rSTG [(62, -16, -2), t=9.81], rMTG [(62, 2, -16), t=9.75] and rSTS [(50, 18, -20), t=7.27]. Frontal activity was seen in dmPFC [(-10, 52, 34), 5.03].

Between-group. In the comparison of ASD > NT, two clusters were significant, one in precuneus [(16, -52, 38), t=5.56] and one in superior/middle frontal gyrus [(24, 20, 44), t=4.73]. No significant results were revealed in the NT > ASD contrast.

Neutral scenarios

ASD. Scenarios of neutral (NEUT) valence (Figure 10 and Appendix H, Table 4), or physical state stories, elicited similar temporal activations associated with inferential language processing in both ASD and NT. Specifically in the autism

group, rightward activations included STS [(52, -12, -6), t=9.39], and on the left, activity was in STS [(-44, -26, 12), t=11.26], MTG [(-62, -14, -4), t=7.90] and in IFG [(-44, 20, 24), t=4.31]. For ToM-related regions, the autism group again showed activity in precuneus [(24, -48, 12), t=3.96]; for emotion-related areas, both left [(-20, -8, -16), t=4.46] and right amygdala [(32, 0, -20), t=3.48] responded to NEUT stories.

NT. Temporal activity for NT in response to the NEUT condition were focused in rSTS [(62, -16, -2), t=9.86] and raSTS [(62, 4, -10), t=7.87)], and also lSTS [(-62, -20, 6), t=9.55], lMTG [(-62, -32, 6), t=9.84] and lIFG [(-44, -40, -20), t=5.51].

Between-group. No contrasts reached significance in group comparisons.

ROI analysis TOM

TOM EMO. Each set of ROI—TOM, NARR and TOM ∩ NARR—were used as implicit masks on 2-sample *t*-tests for EMO, NEG, POS, and NEUT ($p < .002$, $k = 10$). Within TOM ROI (see Figure 10 and Table 15), the EMO contrast revealed large clusters of activation in bTPJ and bSTS for both groups. Activation in ASD was more extensive than controls in TPJ, especially on the left [L: ASD (-48, -70, 22), t=7.07; NT (-52, -64, 20), t=4.95; R: ASD (58, -54, 22), t=6.52; NT (48, -58, 22), t=3.95], whereas activations in STS were more similar in both groups [L: ASD (-54, -30, -4), t=5.36; NT (-54, -30, -4), t=5.44; R: ASD (52, -16, -12), t=5.84; NT (52, -16, -12), t=4.77]. Clusters were also identified in right dmPFC for both [ASD (8, 50, 26), t=3.79; NT (8, 56, 26), t=3.57]. Between-group tests revealed significant activations for ASD > NT, in mPFC [(0, 62, 12), t=3.40], rTPJ [(58, -54, 22), t=3.75], and precuneus [(6, -56, 36), t=4.53]. No significant clusters were revealed in NT > ASD.

TOM NEG. For NEG, regions in bilateral TPJ showed enhanced activity [L: ASD (-56, -58, 18), t=6.61; NT (-58, -50, 22), t=4.67; R: ASD (58, -54, 22), t=6.83; NT (52, -56, -24), t=4.02], as did right IFG [ASD (52, -16, -12), t=6.51; NT (52, -16, -12), t=4.93] and left STS [ASD (-54, -30, -4), t=5.69; NT (-54, -30, -4), t=4.88]. In ASD, a cluster was also revealed in precuneus/aCC [(6, -56, 36), t=5.16] and in rSTS [(6, 50, 24), t=5.23]. No regions were significant for NT that did not also appear in ASD. In ASD > NT, two significant clusters were revealed, in dmPFC [(6, -56, 36), t=5.17] and rTPJ [(60, -52, 22), t=3.90]. Results for NT > ASD failed to reach significance.

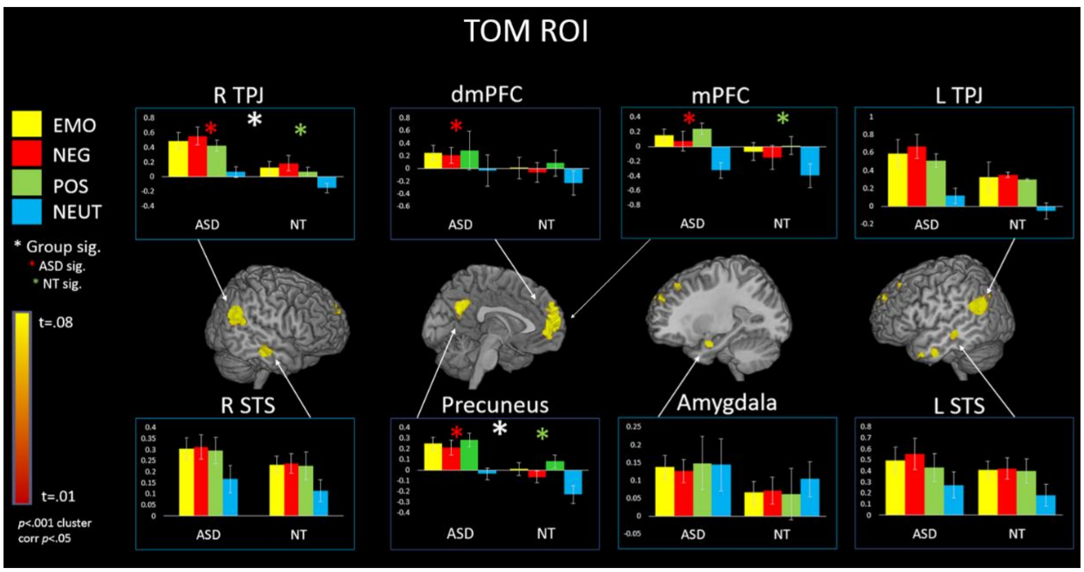


Figure 12. Theory of mind ROI analyses, Study 2. All TOM regions of interest (Mar, 2011) are shown on a template image. Bar graphs show percent signal change in BOLD response to emotion (EMO; yellow), negative (NEG; red), positive (POS; green) and neutral (NEUT; blue) for those ROI yielding significant activation on the *y*-axis, separated by autism (ASD) and neurotypical (NT) groups on *x*-axis. Error bars show standard error. * $p < .05$

TOM POS. Relative to controls, the ASD group also showed more extensive task-related activity for POS scenarios. Like NEG, both groups had significant clusters in lTPJ, rIFG and lSTS. The ASD group had additional activations in dmPFC

[(6, 56, 20), t=3.84] and pCC [(0, -52, 30), t=5.07]. Between-group comparisons yielded no significant findings.

TOM NEUT. For NEUT, activations were in bSTS [L: ASD (-54, -30, -4), t=5.13; NT (-54, -30, -4), t=5.71; R: ASD (50, -18, -10), t=6.32; NT (52, -16, -12), t=4.60] and amygdala [ASD (-28, -2, -22), t=4.67; NT (-28, -2, -22), t=4.10] in both groups, while two clusters in lTPJ [(-56, -60, 18), t=4.73; (-48, -70, 22), t=4.59] showed activity in ASD alone. Between-group tests failed to reach significance.

ROI analysis NARR

NARR EMO. For NARR ROI (see Figure 13 and Table 16) in the EMO contrasts, the largest clusters of activity for ASD and NT were in left STS [ASD (-50, -24, 6), t= 8.89; NT (-62, -20, 6), t=8.53]. Also in LH, IFG (triangularis) was recruited by both groups [ASD (-52, 28, -4), t=5.08; NT (-54, 24, 12), t=4.95]. In the RH, two separate STS clusters were engaged [ASD (58, -12, 4), t=8.43; (58, -8, -20), t=5.53; NT (60, -16, -2), t=8.38; (58, -10, -16), t=4.99], as well as pSTS [ASD (58, -40, 6), t=5.34; NT (52, -42, 6), t=4.56], and aSTS [ASD (56, 6,-20), t=6.42; NT (54, 8, -20), t=7.54]. Other clusters were identified for ASD, two in dmPFC [(-10, 48, 42), t=4.58; (-10, 56, 24), t=3.91] and one in rTPJ [58, -60, 18), t=6.32], while left precentral gyrus [(-48, 0, 52), t=4.26] was additionally recruited by NT. Between-group contrast failed to yield significant results.

Table 15.

ROI results: Theory of mind, Study 2

		ASD						*NT*						*ASD > NT*					
Region	**Lat**	***v***	***x***	***y***	***z***	***t***	***Z***	***v***	***x***	***y***	***z***	***t***	***Z***	***v***	***x***	***y***	***z***	***t***	***Z***
EMO																			
Frontal																			
dmPFC	R	67	8	50	26	3.79	3.38	18	8	56	26	3.57	3.21						
Temporal																			
TPJ	L	336	-48	-70	22	7.07	5.31	133	-52	-64	20	4.95	4.16						
[a]	L	[a]	-56	-60	20	5.99	4.77	[a]	-58	-50	22	4.43	3.82						
[a]	L	[a]	-42	-58	24	4.8	4.07	[a]	-48	-54	22	4.02	3.54						
[a]	L	[a]	-54	-64	34	3.96	3.5	[a]	-42	-64	24	3.99	3.52						
	L	17	-44	-72	38	4.17	3.65												
	R	243	58	-54	22	6.52	5.04	22	48	-58	22	3.95	3.49	17	58	-54	22	3.75	3.35
STS	R	88	52	-16	-12	5.84	4.68	71	52	-16	-12	4.77	4.04						
[a]	R	[a]	56	-8	-20	4.82	4.08	[a]	58	-10	-18	4.62	3.95						
STS	L	27	-54	-30	-4	5.36	4.41	19	-54	-30	-4	5.44	4.46						
Parietal																			
pCC	-	177	0	-52	30	5.27	4.36							24	6	-56	36	4.53	3.89
Precuneus	L	[a]	-12	-54	34	4.22	3.68												
NEG																			
Frontal																			
dmPFC	R							10	6	52	28	3.55	3.2						
Temporal																			
TPJ	R	259	58	-54	22	6.83	5.2	21	52	-56	24	4.02	3.54	15	60	-52	22	3.9	3.46
[a]	L	346	-56	-58	18	6.61	5.09	100	-58	-50	22	4.67	3.98						
[a]	L	[a]	-46	-68	22	6.59	5.08	[a]	-52	-62	18	4.63	3.95						
[a]	L	[a]	-60	-52	26	4.31	3.74												
MOcc	L	[a]	-42	-56	26	4.7	4												
[a]	L	[a]	-54	-64	32	3.47	3.14												
IFG	R	81	52	-16	-12	6.51	5.04	62	52	-16	-12	4.93	4.15						
[a]	R	[a]	58	-10	-18	4.93	4.15	[a]	58	-10	-18	4.26	3.71						
STS	L	29	-54	-30	-4	5.69	4.6	13	-54	-30	-4	4.88	4.12						
[a]	R	77	6	50	24	5.23	4.33												

		ASD						*NT*						*ASD > NT*					
Region	**Lat**	***v***	***x***	***y***	***z***	***t***	***Z***	***v***	***x***	***y***	***z***	***t***	***Z***	***v***	***x***	***y***	***z***	***t***	***Z***
Parietal																			
Precuneus	R	106	6	-56	36	5.16	4.29							42	6	-56	36	5.17	4.29
aCC	L	[a]	-12	-54	34	4.14	3.63												
POS																			
Frontal																			
dmPFC	R	10	6	56	20	3.84	3.41												
[a]	R	12	10	54	30	3.71	3.32												
Temporal																			
TPJ	R	209	58	-60	18	7.25	5.4												
[a]	R	[a]	46	-56	26	4.64	3.96												
	L	263	-48	-70	22	6.95	5.26	71	-50	-66	20	5.39	4.43						
[a]	L	[a]	-56	-60	18	6.58	5.07	[a]	-46	-56	22	3.51	3.17						
[a]	L	[a]	-54	-64	34	4.48	3.86												
[a]	L	[a]	-60	-52	24	3.52	3.18												
MOcc	L	[a]	-42	-62	24	5.29	4.37												
IFG	R	79	52	-16	-12	6.35	4.96	70	52	-16	-12	5.01	4.2						
[a]	R	[a]	58	-10	-20	5.15	4.29	[a]	58	-10	-18	4.87	4.11						
STS	L	23	-54	-30	-4	5.81	4.66	21	-54	-30	-4	6.16	4.86						
MOcc	L	17	-44	-72	38	4.82	4.08												
Parietal																			
pCC	-	215	0	-52	30	5.07	4.24												
[a]	L	[a]	-12	-54	34	4.55	3.91												
NEUT																			
Temporal																			
STS	R	56	50	-18	-10	6.32	4.94	45	52	-16	-12	4.6	3.94						
[a]	R	[a]	56	-8	-20	4.09	3.59	[a]	58	-10	-18	3.71	3.32						
	L	14	-54	-30	-4	5.13	4.27												
TPJ	L	21	-56	-60	18	4.73	4.02												
	R	33	58	-60	16	4.01	3.54												
Limbic																			
Amygdala	L							10	-28	-2	-22	4.1	3.6						

Note. T-values for signal increases in TOM ROI in emotion (EMO), negative (NEG), positive (POS) and neutral (NEUT) for autism (ASD), neurotypical (NT) and NT > ASD. No significant clusters were found in NT > ASD comparison. Laterality (Lat) right (R), left (L) or medial ('-'), number of voxels in each cluster (*v*), XYZ coordinates, *t*-values and *z*-scores. Coordinates are MNI space. Height threshold EMO, $t = 3.24$; NEG, $t = 3.41$; POS, $t = 3.18$; NEUT, $t = 3.41$; $p < .002$, $k = 10$.

[a] Subpeaks of larger cluster immediately above.

NARR NEG. For both ASD and NT, most extensive activations for negative stories were in lSTS (ASD (-50, -24, 6), t=11.21); NT (-62, -20, 6), t=9.14], with two much smaller clusters in rSTS [ASD (56, -12, 6), t=9.93; (58, -40, 6), t=6.06; NT (60, 16, -2), t=8.91; (58, -10, -16), t=5.00]. Both groups also had significant clusters in lIFG [ASD (-46, 22, 20), t=4.80; NT (-52, 24, 10), t=4.65]. The autism group also showed significant activity in rTPJ [(56, -60, 18), t=6.02] and dmPFC [(-8, 56, 26), t=3.50], while the controls recruited a region in aSTS [(54, 6, -20), t=7.23] and precentral gyrus [(-48, 0, 52), t=3.93]. No significant activity was shown in between-group tests.

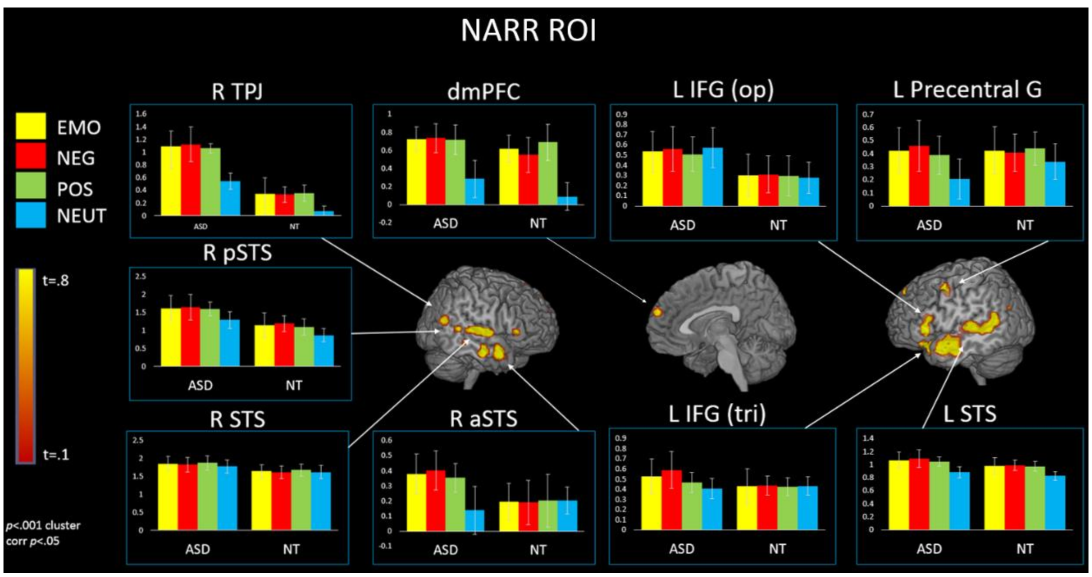


Figure 12. Narrative ROI analyses, Study 2. All NARR regions of interest (Mar, 2011) are shown on a template image. Bar graphs show percent signal change in BOLD response to emotion (EMO; yellow), negative (NEG; red), positive (POS; green) and neutral (NEUT; blue) for those ROI yielding significant activation on the *y*-axis, separated by autism (ASD) and neurotypical (NT) groups on *x*-axis. Error bars show standard error.

Table 16.

ROI results: Narrative, Study 2

Region	Lat	***ASD*** *v*	*x*	*y*	*z*	*t*	*Z*	***NT*** *v*	*x*	*y*	*z*	*t*	*Z*
EMO													
Frontal													
dmPFC	L	11	-10	48	42	4.58	3.92						
	L	31	-10	56	24	3.91	3.47						
Precentral gyrus	L							36	-48	0	52	4.26	3.71
Temporal													
STS	L	1688	-50	-24	6	8.89	6.08	1558	-62	-20	6	8.53	5.94
[a]	L	[a]	-62	-14	-4	7.50	5.51	[a]	-62	-32	6	8.49	5.93
[a]	L	[a]	-62	-42	4	7.36	5.44	[a]	-52	-28	2	8.29	5.84
[a]	L	[a]	-46	12	-26	7.12	5.34	[a]	-62	-10	-12	8.08	5.76
[a]	L	[a]	-64	-28	8	6.69	5.13	[a]	-54	12	-14	7.22	5.38
STS	R	303	58	-12	4	8.43	5.90	327	60	-16	-2	8.38	5.88
[a]	R	[a]	54	-22	2	6.91	5.24	[a]	54	-14	6	7.19	5.37
[a]	R	[a]	50	-32	8	6.18	4.87	[a]	58	-2	-2	6.96	5.26
[a]	R	[a]	58	-2	-6	5.64	4.57	[a]	54	-30	6	6.51	5.04
IFG (opercularis)	R	278	56	6	-20	6.42	4.99	198	54	8	-20	7.54	5.53
a	R	[a]	40	20	-32	4.02	3.54	[a]	38	18	-34	4.67	3.98
a	R	[a]	48	6	-30	3.60	3.24						
TPJ	R	77	58	-60	18	6.32	4.94						
STS	R	51	58	-8	-20	5.53	4.51	22	58	-10	-16	4.99	4.19
pSTS	R	36	58	-40	6	5.34	4.4	29	52	-42	6	4.56	3.91
IFG (triangularis)	L	31	-52	28	-4	5.08	4.24	107	-54	24	12	4.95	4.16
								[a]	-56	32	6	4.39	3.8
IFG (opercularis)	L	115	-46	22	20	5.07	4.24						
[a]	L	[a]	-54	26	12	4.35	3.77						
NEG													
Frontal													
dmPFC	L	24	-8	56	26	3.5	3.16						
Precentral	L							14	-48	0	52	3.93	3.47
Temporal													
STS	L	1680	-50	-24	6	11.21	6.85	1483	-62	-20	6	9.14	6.17
[a]	L	[a]	-62	-14	-4	8.78	6.04	[a]	-62	-32	6	8.68	6
[a]	L	[a]	-62	-42	4	7.86	5.67	[a]	-50	-26	4	8.6	5.97
[a]	L	[a]	-64	-28	8	7.78	5.63	[a]	-60	-8	-12	7.74	5.61

Region	Lat	ASD						NT					
		v	***x***	***y***	***z***	***t***	***Z***	***v***	***x***	***y***	***z***	***t***	***Z***
[a]	L	[a]	-46	12	-26	7.34	5.44	[a]	-54	12	-14	6.45	5.01
	R	305	56	-12	6	9.93	6.45	319	60	-16	-2	8.91	6.09
[a]	R	[a]	54	-30	6	7.82	5.65	[a]	58	-2	-2	6.95	5.26
[a]	R	[a]	62	-22	6	7.22	5.38	[a]	54	-30	6	6.75	5.16
[a]	R	[a]	58	-2	-6	6.22	4.89						
MTG	R	328	56	6	-20	7.17	5.36						
[a]	R	[a]	50	14	-26	6.23	4.89						
[a]	R	[a]	42	12	-34	4.25	3.7						
[a]	R	[a]	50	4	-28	3.83	3.4						
STS	R	36	58	-40	6	6.06	4.8	15	58	-10	-16	5	4.19
TPJ	R	77	56	-60	18	6.02	4.78						
IFG (triangularis)	L	40	-52	28	-4	5.38	4.42						
STS	R	52	58	-10	-16	5.28	4.36	30	52	-42	6	4.51	3.88
[a]	R	[a]	60	-2	-22	5.06	4.23						
IFG (triangularis)	L	107	-46	22	20	4.8	4.07	68	-52	24	10	4.65	3.97
[a]	L	[a]	-54	26	12	4.73	4.02						
	L	13	-46	26	-8	3.66	3.28						
IFG (opercularis)								193	54	6	-20	7.23	5.39
[a]								[a]	38	18	-34	4.71	4.01
[a]								[a]	50	16	-26	4.64	3.96
POS													
Frontal													
dmPFC	L	13	-12	50	42	4.71	4	15	-10	48	42	4.33	3.76
	L	32	-8	58	22	3.74	3.34						
Precentral								47	-48	0	52	4.44	3.83
Temporal													
STS	L	1688	-50	-24	6	11.88	7.04	1545	-58	-22	8	9.83	6.41
[a]	L	[a]	-62	-14	-4	8.8	6.05	[a]	-62	-32	8	9.16	6.18
[a]	L	[a]	-62	-42	4	8.3	5.85	[a]	-60	-14	-12	9.15	6.18
[a]	L	[a]	-64	-26	8	8.09	5.76	[a]	-52	-28	2	8.79	6.04
[a]	L	[a]	-54	12	-14	6.86	5.21	[a]	-54	12	-14	8.09	5.76
	R	317	52	-12	4	10.59	6.66	334	60	-18	0	9.46	6.29
[a]	R	[a]	54	-22	2	8.32	5.86	[a]	52	-12	4	8.51	5.93
[a]	R	[a]	50	-32	8	7.69	5.59	[a]	58	-2	-2	7.3	5.42
[a]	R	[a]	58	-2	-6	6.39	4.98	[a]	50	-32	8	7.01	5.28
TPJ	R	77	60	-62	16	7.63	5.57						
IFG (opercularis)	R	246	56	6	-20	7.32	5.43	179	56	6	-20	7.9	5.68

Region	Lat	*ASD*						*NT*					
Region	**Lat**	***v***	***x***	**Region**	**L**	***v***	***x***	**Region**	**L**	***v***	***x***	**Region**	**L**
[a]	R	[a]	40	20	-32	4.44	3.83	[a]	52	16	-26	5.8	4.66
[a]	R							[a]	40	20	-32	3.8	3.39
STS	R	36	56	-44	6	5.99	4.77	30	52	-42	6	4.71	4.01
MTG	R	48	58	-8	-20	5.76	4.64	27	58	-8	-16	5.14	4.28
IFG (triangularis)	L	88	-46	22	20	4.98	4.18	119	-54	24	12	5.04	4.22
[a]	L							[a]	-52	24	0	3.91	3.46
NEUT													
Frontal													
Precentral	L							27	-48	-2	52	4.15	3.63
Temporal													
STS	L	1311	-50	-24	6	10.79	6.73	1264	-62	-32	6	9.84	6.42
[a]	L	[a]	-64	-28	8	7.91	5.69	[a]	-62	-20	6	9.55	6.32
[a]	L	[a]	-62	-14	-4	7.90	5.68	[a]	-52	-22	4	8.97	6.11
[a]	L	[a]	-62	-40	4	7.03	5.29	[a]	-58	-6	-14	7.57	5.54
[a]	L	[a]	-52	8	-14	6.48	5.02	[a]	-60	-10	-4	7.03	5.29
STS	R	301	54	-14	6	10.42	6.61	335	62	-18	0	9.24	6.21
[a]	R	[a]	62	-22	6	7.37	5.45	[a]	54	-14	6	8.69	6.00
[a]	R	[a]	54	-30	6	7.30	5.42	[a]	58	-2	-2	7.06	5.31
[a]	R	[a]	58	-2	-6	6.48	5.02	[a]	54	-30	6	6.76	5.16
pSTS	R	36	58	-40	6	5.81	4.67						
IFG (opercularis)	R	90	54	14	-20	5.70	4.61	77	56	8	-20	5.46	4.47
	R							[a]	50	16	-24	4.18	3.65
IFG (triangularis)	L	80	-46	24	20	4.85	4.10	94	-56	30	6	4.14	3.63
[a]	L	[a]	-54	26	14	3.69	3.30	[a]	-46	32	4	4.13	3.62
STS	R	29	58	-10	-16	4.31	3.74	11	58	-10	-16	4.65	3.97
TPJ	R	33	58	-60	16	4.01	3.54	20	52	-42	6	4.03	3.55

Note. *T*-values for signal increases NARR ROI for emotion (EMO), negative (NEG), positive (POS) and neutral (NEUT) scenarios for ASD (autism group) and NT (neurotypical control group). No significant clusters were found in ASD > NT or NT > ASD comparisons. Laterality right (R) or left (L). Number of voxels in each cluster (*v*), XYZ coordinates, *t*-values and *z*-scores. Coordinates are MNI space. Height threshold EMO, $t = 3.24$; NEG, $t = 3.41$; POS, $t = 3.18$; NEUT, $t = 3.41$; $p < .002$, $k = 10$.

[a] Subpeaks of larger cluster immediately above.

NARR POS. Neural activations in response to POS stories in the NARR regions of interest were highly similar between groups and also to the NEG condition. Extensive temporal activations were seen in lSTS [ASD (-50, -24, 6), t=11.88; NT (-58, -22, 8) t=9.83] for both groups, with smaller clusters in rSTS. Both ASD and NT also recruited bilateral aSTS [ASD (56, 6, -20), t=7.32); NT (56, 6, -20), t=7.90)], IFG (triangularis) [ASD (-46, 22, 20), t=4.18; NT (-54, 24, 12), t=5.04)] and dmPFC [ASD (-12, 50, 42), t=4.71; NT (-10, 48, 42), t=4.33]. As with NEG, ASD engaged rTPJ [(60, -62, 16), t=7.63], and NT recruited precentral gyrus [(-48, 0, 52), t=4.44].

Direct comparisons between groups failed to reach significance.

NARR NEUT. In the NEUT contrast, narrative ROIs with the largest activity in both groups included STS bilaterally, with largest clusters in the left hemisphere [ASD (-50, -24, 6), t=10.93; NT (-62, -32, 6), t=9.84]. On the right, two separate clusters were shown in STS [ASD (54, -14, 6), t=10.42; (58, -10, -16), t=4.31; NT (62, -18, 0), t=9.24; (58, -10, -16), t=4.65], and TPJ [ASD (58, -10, 16), t=4.01; NT (52, -42, 6), t=4.03] for both groups, and the autistic participants also revealed rightward pSTS activity [(58, -40, 6), t=5.81]. Inferior/frontal clusters were also identified in both groups: left IFG (triangularis) (ASD (-46, 24, 20), t=4.85; NT (-56, 30, 6), t=4.14], and right aSTS (ASD (54, 14, -20), t=5.70; NT (56, 8, -20), t=5.46]. Lastly, as in the EMO condition, left precentral gyrus was recruited in the control group [(-48, -2, 52), t=4.15]. Between-group contrasts yielded no significant results.

ROI Analysis TOM ∩ NARR

TOM ∩ NARR EMO. Within the ROIs associated with both ToM and narrative comprehension (see Figure 13 and Table 17), EMO scenarios evoked lTPJ

bilaterally in both groups [ASD (-56, -58, 18), t=5.94; NT (-58, -52, 22), t=4.33], while right hemisphere clusters in both TPJ [(58, -60, 18), t=6.32] and MTG [(56, -8, -20), t=4.82] were additionally recruited by the ASD group. Between-groups test were not significant.

TOM ∩ NARR NEG. Like EMO, NEG scenarios were associated with significant activity in lTPJ for both groups [ASD (-56, -58, 18), t=6.61; NT (-56, -52, 20), t=4.48], while rTPJ [(56, -60, 18), t=6.02] and rMTG [(58, -10, -18), t=4.93] were also significantly engaged in the autism group. Between-group contrasts showed no effects.

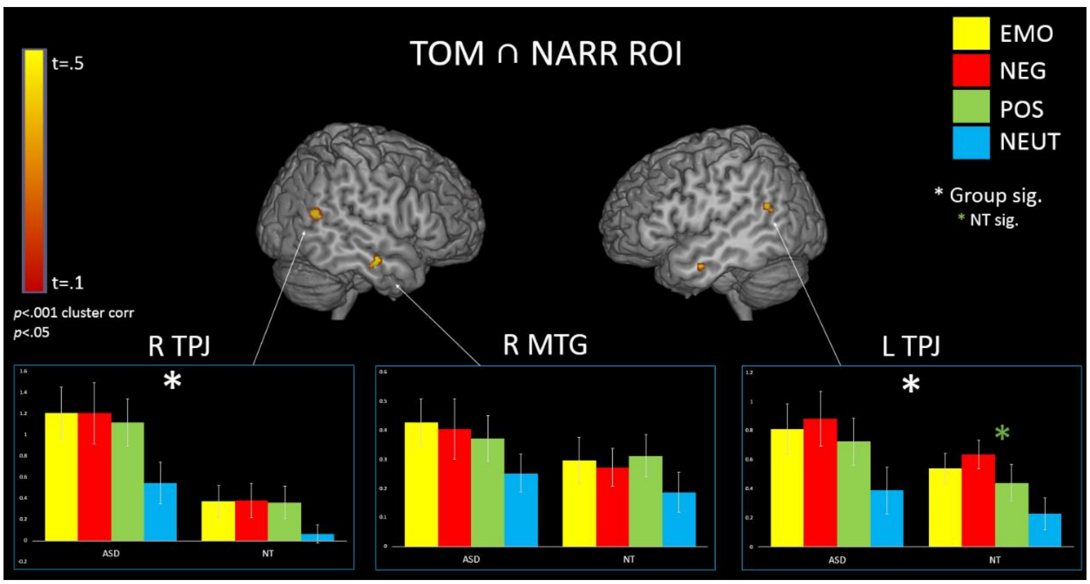


Figure 13. ToM ∩ NARR (ROI) analyses, Study 2. All regions of interest in ToM ∩ NARR (Mar, 2011) are shown on a template image. Bar graphs show percent signal change in BOLD response to EMO (yellow), NEG (red), POS (green) and NEUT (blue) for those ROI yielding significant activation on the *y*-axis, separated by ASD and NT groups on *x*-axis. In right TPJ (*), activations to both EMO and NEUT for ASD are significantly greater than in NT. Error bars show standard error.
* $p < .05$

Table 17.

ROI results: TOM ∩ NARR, Study 2

		ASD						***NT***					
Region label	L	*v*	*x*	*y*	*z*	*t*	*Z*	*v*	*x*	*y*	*z*	*t*	*Z*
EMO													
Temporal													
TPJ	R	50	58	-60	18	6.32	4.94						
	L	24	-56	-58	18	5.94	4.74	18	-58	-52	22	4.33	3.75
	L							*a*	-52	-54	20	3.90	3.46
MTG	R	11	56	-8	-20	4.82	4.08						
NEG													
Temporal													
TPJ	L	26	-56	-58	18	6.61	5.09	20	-56	-52	20	4.48	3.86
	R	50	56	-60	18	6.02	4.78						
MTG	R	11	58	-10	-18	4.93	4.15						
POS													
Temporal													
TPJ	R	50	58	-60	18	7.25	5.4						
	L	23	-56	-58	18	6.29	4.93						
MTG	R	11	58	-10	-20	5.15	4.29						
NEUT													
Temporal													
TPJ	R	22	58	-60	16	4.01	3.54						

Note. We show *t*-values for signal increases in the conjunction of theory of mind and narrative (TOM ∩ NARR) regions of interest for emotion (EMO), negative (NEG), positive (POS) and neutral (NEUT) scenarios for ASD (autism group) and NT (neurotypical control group). No other contrasts revealed significant activations. Laterality (Lat) right (R) or left (L), number of voxels in each cluster (Voxel), XYZ coordinates, *t*-values and *z*-scores. Coordinates are MNI space. Height threshold EMO, $t = 3.24$; NEG, $t = 3.41$; POS, $t = 3.18$; NEUT, $t = 3.41$; $p < .002$, $k = 10$.

[a] Subpeaks of larger cluster immediately above.

TOM ∩ NARR POS. While the controls did not show any significant activity in clusters associated with both TOM and NARR, the autism participants showed significant activity in TPJ bilaterally [L (-56, -58, 18), t=6.29; R (58, -60, 18), t=7.25] and rMTG [(58, -10, -20), t=5.15]. Comparisons between groups were not significant.

TOM ∩ NARR NEUT. For NEUT, a significant cluster was revealed for ASD in rTPJ [(58, -60, 16), t=4.01]. No significant between group effects were revealed.

ROI statistical analyses

Between-group. Between-group comparisons for TOM ∩ NARR ROI revealed significant group effect for valence, $F(2, 56) = 3.890$, $p = .026$, pairwise comparisons showed that NEG stories for ASD were significantly greater than NT in lTPJ, and in rTPJ, both POS and NEUT were greater for ASD compared to NT. While RM ANOVA failed to yield significant any group x condition interactions, but rTPJ neared significance, with a moderate effect size $F(1,28) = 3.12$, $p = .089$, $r = .32$.

For TOM ROI, RM ANOVA revealed significant group x condition effects in precuneus for NEG, $F(1,28) = 9.223$, $p = .005$ and POS, $F(1,28) = 5.601$, $p = .025$, and in rTPJ for NEG, $F(1,28) = 7.253$, $p = .012$, and POS ($F(1,28) = 8.068$, $p = .008$). In both, ASD had enhanced activity relative to NT. No significant group * valence interactions were shown.

No significant main effects were revealed for NARR ROI.

Within-group. Follow-up contrasts within groups (corrected using Tukey's test to control for multiple contrasts) showed that for TOM ∩ NARR, a significant effect of condition was shown lTPJ ($F(2, 45) = 3.299$, $p = .046$) for the NT group, such than NEUT had less activation than NEG. In TOM ROI, a significant effect of

condition was seen in midline structures for both groups, mPFC (ASD $F(2, 39) = 7.315$, $p = .002$; NT $F(2, 45) = 3.292$, $p = .046$) and precuneus (ASD $F(2, 39) = 6.554$, $p = .004$; NT $F(2, 45) = 4.471$, $p = .017$), where the effects were between conditions was driven by the deactivation in NEUT relative to activity in POS and NEG. Significant differences were also found in rTPJ (ASD $F(2, 39) = 5.339$, $p = .009$; NT $F(2, 45) = 7.338$, $p = .002$), where both POS and NEG had more activity than NEUT, and the same effect was seen for the control group in lTPJ ($F(2, 45) = 3.371$, $p = .043$). Tests for NARR regions of interest failed to reach significance.

Brain-behavior relationships were explored by comparing the parameter estimates from within-group single sample *t*-tests for individual TOM ROI in POS, NEG and NEUT contrasts with scores from the cognitive and social-affective assessments. See Appendix I, Tables 1 (ASD) and 2 (NT) for summary correlations, and Figure 14 for illustrations of effects for social-affective assessments. (Correlations for cognitive measures are not illustrated due to significant relationships between cognitive and social-affective tests in the NT group.) Activations in the amygdala ROI for POS were significantly related to scores from Mind in the Eyes ($r = .518$, $p = .029$, $n = 14$), AQ ($r = -.606$, $p = .022$, $n = 14$) and EQ ($r = .681$, $p = .007$, $n = 14$). Herein, all tests shared the same trend, i.e., greater social-affective impairments predicted lower amygdala engagement. Other significant associations were between mPFC and the EQ ($r = .640$, $p = .014$, $n = 14$) (following the same pattern of greater impairments predicting lower activation), and rTPJ with WRAML scores ($r = .650$, $p = .012$, $n = 14$). The latter showing a positive relationship between

better sentence repetition ability and more right temporal activity for POS scenarios. No significant correlations were shown in either NEG or NEUT contrasts for ASD.

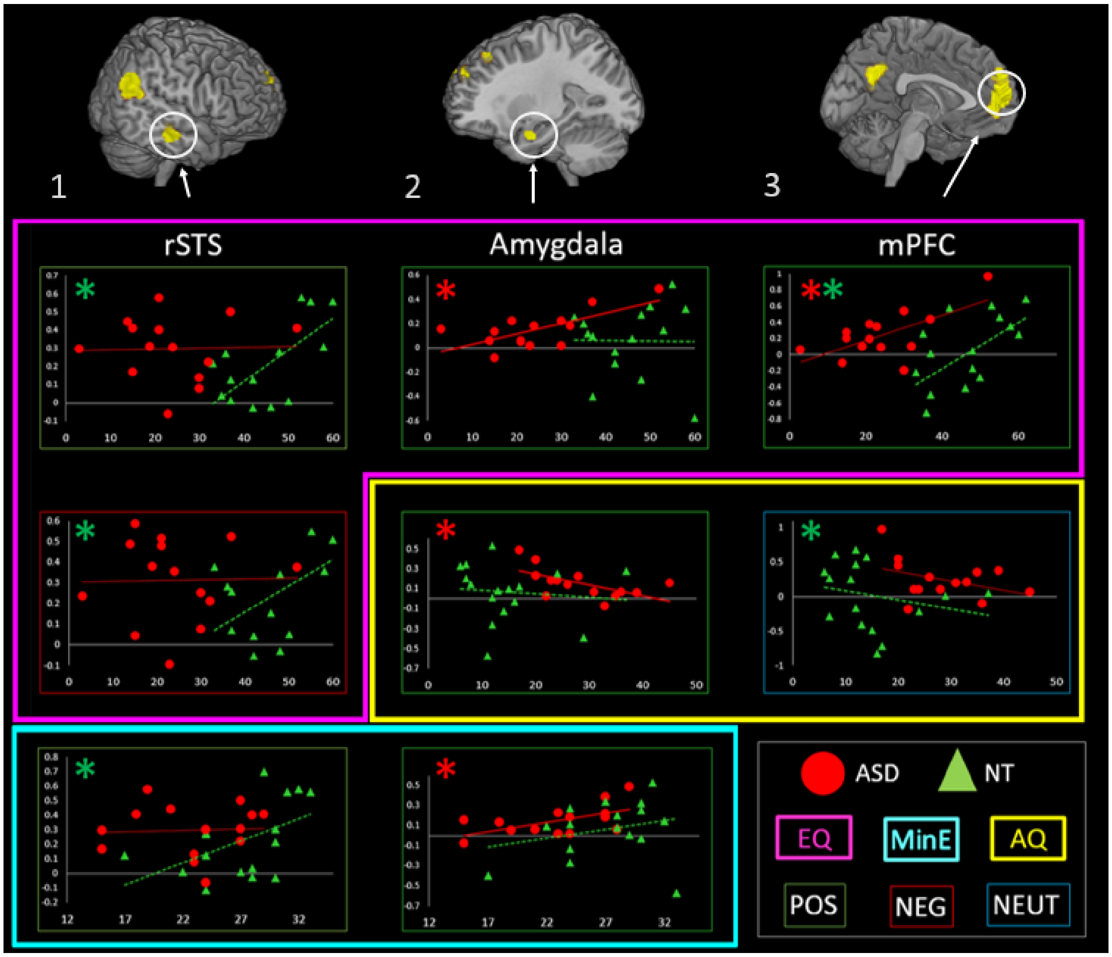


Figure 14. Brain-behavior correlations TOM ROI, Study 2. Scatterplots showing relationship between social-affective behavioral measure on *x*-axis and parameter estimates from 1-sample within group *t*-tests (*y*-axis) in autism (ASD, red '◯') and neurotypical controls (NT; green 'Δ'). Pink box: scores for Empathy Quotient (EQ) and rSTS (POS, A1; NEG, B1), amygdala (A2) and mPFC (A3) such that higher EQ scores indicate better ability to empathize and predict enhanced neural activation. Yellow box: the Autism Quotient (AQ) and amygdala (B2) and mPFC (B3), where higher scores indicate more autistic symptomatology and predict decreases in brain activity. Aqua box: scores from Mind in the Eyes (MinE) and rSTS (C1) and amygdala (C2), here higher scores specify better mentalizing abilities from judging photos of eyes and predict greater BOLD activation. Each scatterplot shows a correlation significant in at least one group (ASD, '*'; NT, '*'), with the other group plotted for between-group comparisons. Outline around each plot indicates contrast in which significant correlations occurred, positive (POS; green), negative (NEG; red), or neutral (NEUT; blue).

The control group had significant correlation tests for POS stories in rSTS, where WRAML (r = .652, p = .006, n = 16), Mind in Eyes (r = .502, p = .047, n =

16), and EQ (*r* = .645, *p* = .007, *n* = 16); in each, greater impairment correlated with lower neural activations. Other significant relationships were found between IQ and rTPJ (*r* = -.526, *p* = .036, *n* = 16), and EQ and mPFC (*r* = .568, *p* = .022, *n* = 16). In each of these regions, ability was reflected in lower neural responses. In contrast, in the test between WJIII and amygdala (*r* = .535, *p* = .033, *n* = 16), where better oral language skills correlated with enhanced activations.

Also in NT, for NEG scenarios a significant correlation was revealed between EQ and rSTS (*r* = .532, *p* = .034, *n* = 16), such that (like POS) greater ability predicted enhanced neural activity. Lastly, for NEUT stories, AQ was negatively related to mPFC activation (*r* = -.518, *p* = .040, *n* = 16), i.e., greater impairments were suggestive of lower activations.

Target probe results

For the response epoch, between-group comparisons revealed similar neural activations in both groups, and these were predominantly in occipital- and motor regions. There was a significant interaction effect in the negative congruent (NegCon) & incongruent (NegIncon) conditions however, perhaps mirroring the behavioral effects in response time (see Figure 9). The largest areas with significant interaction effects were both located in mPFC [(-4, 48, 40), *F*=21.77); (-4, 34, 54), *F*=18.59)] and included aCC, followed by frontal right angular gyrus [(44, 50, 26), *F*=23.96] and aCC [(12, 46, 2), *F*=26.61]. In each, the ASD group had greater activations to the NegIncon compared to the NegCon stories, while the NT group showed the reverse, with greater activations to the NegCon than NegIncon. (See Figure 15 and Table 18).

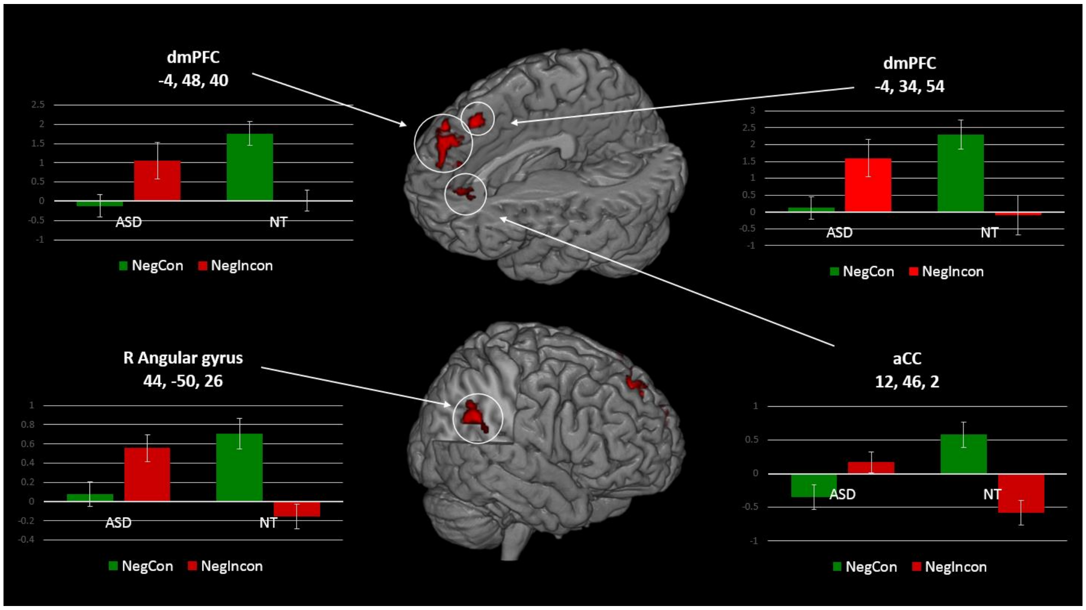


Figure 15. Interaction effect in target probe, Study 2. Regions showing significant activation in negative congruent (NegCon; green) and negative incongruent (NegIncon; red) interaction. Task-related activity is displayed using a threshold of p < .001 corrected with cluster extent FWE threshold (p<0.05) for F-statistic maps. Coordinates in Montreal Neurologic Institute (MNI) space. Error bars show standard error.

Table 18.

Interaction effect: negative congruent & incongruent probe, Study 2

Region label	Lat	*voxels*	*x*	*y*	*z*	*F*	*Z*
ASD							
Frontal							
aCC	R	96	12	46	2	26.61	4.83
dmPFC	-	635	-4	48	40	21.77	4.37
[a]	L	[a]	-10	60	20	21.77	4.33
[a]	R	[a]	14	46	46	18.38	4.01
[a]	L	[a]	-12	40	40	20.48	4.24
aCC	L	[a]	-10	42	12	16.51	3.79
dmPFC	-	178	-4	34	54	18.59	4.03
[a]	R	[a]	6	26	50	15.64	3.69
[a]	L	[a]	-14	26	60	15.10	3.62
Parietal							
Angular gyrus	R	114	44	-50	26	23.96	4.58

Note. We show F-values for signal increases for the interaction effect in negative congruent (NegCon) and negative incongruent (NegIncon) target probe condition. Laterality (Lat) right (R) or left (L), number of voxels in each cluster (Voxel), XYZ coordinates, t-values and z-scores. Coordinates are MNI space. Height threshold F = 11.22, p < .001 corrected with cluster extent FWE threshold (p<0.05).
[a] Subpeaks of larger cluster immediately above.

Discussion

In the present study, the performance of autistic individuals was compared to a neurotypical group while they listened to short vignettes and made judgements concerning the feelings of the protagonist. The scenarios were devoid of explicitly emotional words and/or prosody, and as such required the listener to infer such states from the contextual information alone. Neural activations were characterized during two epochs: hearing the scenarios (POS, NEG, or NEUT), and also during the response to a related T/F question. Accuracy and response time were recorded. For both ASD and NT, behavioral and neural results show participants' reactions varied depending on valence and also congruency, but with differential effects. With respect to the behavioral effects, both groups showed overall faster and more accurate responses to EMO relative to NEUT scenarios, as well as for CON compared to INCON judgments. However, in comparison to the controls, the ASD group showed greater difficulty (i.e., slower and less accurate responses) for INCON judgements, especially in the NEG and NEUT conditions of valence. Brain responses of the ASD group also differed from controls. Here, the main findings reveal similar patterns between groups, but increased activation in individuals with ASD in regions associated with theory of mind processing for emotional but not neutral scenarios, especially right TPJ and precuneus where significant between-group effects were shown. In contrast, no significant effects were seen in ROIs associated with narrative comprehension. Brain-behavior correlations showed that greater recruitment of rSTS was related to better social abilities in controls, but this effect was not seen in ASD. Amygdala and mPFC were differentially recruited in ASD, here too improved social

skills predicted greater activations, but for autism. Overall, these results suggest that making language-based emotional ToM inferences engage social-affective brain regions differentially depending on valence in autistic individuals.

Emotional facilitation in ASD, but inflated effect of congruency

In line with previous research, it was predicted that the autism group would show overall slower response times to the T/F target, but otherwise would exhibit similar characteristics to the control group, specifically: 1) accurate identification, 2) faster responses to emotional compared with neutral scenarios, and 3) faster responses to congruent relative to incongruent targets. The findings generally support these predictions, suggesting that individuals with autism *are* able to use information from verbal scenarios to infer the feelings of a protagonist, even when devoid of emotionally explicit language. However, there are differential effects between patterns seen in RTs and accuracy scores, showing that congruency judgments were particularly challenging, especially in terms of accuracy when deciding on responses that were incongruent with the expected emotional state implied by the negative and neutral scenarios.

A chief finding from these behavioral results was that response times generally indicated that emotional scenarios were more salient than neutral for ASD, in line with previous research showing emotional facilitation effects in typical participants (faster RT and greater accuracy to emotional stimuli) (Eviatar & Zaidel, 1991; Herbert et al., 2005; Kensinger & Corkin, 2003; Kissler & Koessler, 2011; Kousta et al., 2009; Kuchinke, Võ, Hofmann, & Jacobs, 2007). These results contradict other research in autism where emotional facilitation effects are absent, and

this may be due to task differences. The response epoch required participants to respond to a three-word T/F question (*"He felt happy."*). As such, the task is similar to other receptive language studies where autistic individuals show competence (Catarino et al., 2011; Downs & Smith, 2004; Hillier & Allinson, 2002; Lartseva, Dijkstra, & Buitelaar, 2015; Loveland et al., 1997; Rieffe et al., 2000; Rieffe et al., 2007). By contrast, studies investigating affective language showing a *lack* of emotional facilitation effects in ASD involve memory or more complicated detection processes (Beversdorf et al., 1998; Corden et al., 2008; Gaigg & Bowler, 2009a, 2009b; Gaigg, Gardiner, & Bowler, 2008; Grossman et al., 2000; Han et al., 2014; Kennedy et al., 2006; Lindner & Rosén, 2006; but see South et al., 2008).

A second key finding lies within the differential effects seen in accuracy for congruency judgments. The overall trend for both groups showed that CON was processed more easily than INCON, consistent with literature regarding conflict monitoring in neurotypical groups (Botvinick et al., 2001; Ochsner et al., 2009). However, the ASD group had significantly greater difficulty judging the INCON responses for NEG and NEUT relative to controls, and also to the POS condition. Interestingly, they showed the opposite pattern for accuracy in POS, where PosIncon had slightly higher accuracy scores than PosCon (but results were not significant). Within-group ANOVA results (Table 14) reveal that for accuracy in the ASD group, there was a main effect of congruency, and the main effect for both valence and valence x congruency neared significance. In contrast, within-group comparisons for NT revealed greater similarities for accuracy across conditions, suggesting the interaction effects between groups may be actualized with increased statistical power.

Task difficulty may also proffer an explanation for the lower accuracy the autistic group showed in the NegIncon and NeutIncon judgments. Autistic individuals show increased impairment in the face of inconsistencies or when faced with multiple cues (Downs & Smith, 2004; Fink et al., 2014; Grossman et al., 2000; Hobson & Lee, 1989; Lindner & Rosén, 2006). The fact that the same pattern was not seen between the PosCon and PosIncon condition may have several explanations. Firstly, there may be an enhanced effect of familiarity or predictability in the positive scenarios and/or target response words for the autistic participants, facilitating both the congruent and incongruent responses. Data from Study 1 as well as the controls in Study 2 suggests positive scenarios were the easiest, even in the incongruent condition.

Another reason for the differential accuracy effects may be the effect of positive and negative valence, but research delineating the two in autism are scarce (many studies using only negative and neutral stimuli, e.g., Beversdorf et al. 1998). One study reveals intact abilities for identifying positive emotional words but not negative (Rieffe et al., 2007), but in a lexical decision task, RTs were equivalent to both positive and negative words (Lartseva et al., 2015). Further, an investigation using pictures failed to show enhanced recall for either positive or negative pictures in autistic individuals (Deruelle et al., 2008). In typical participants, there seems to be a facilitation effect for positive over negative valence: positive words are recalled more often than neutral (Kissler, Herbert, Winkler, & Junghofer, 2009; but see Kissler, Herbert, Peyk, & Junghofer, 2007) and positive words are identified more quickly than negative (Dahl, 2001; Estes & Adelman, 2008; Kissler & Koessler, 2011; McKenna & Sharma, 1995; Williams, Mathews, & MacLeod, 1996). However,

in detection tasks, negative faces evoked faster reactions than positive (Ohman, Lundqvist, & Esteves, 2001), and responses to negative words were faster than positive, and were identified with greater accuracy (Nasrallah, Carmel, & Lavie, 2009). More research concerning the differential effects of valence is necessary to disentangle the saliency of positive and negative in autism.

In light of the contradictory behavioral literature regarding emotional language understandings in autism, these results generally support the notion of intact abilities understanding others' feelings from the language context, even when not explicitly stated, and without prosodic cues. Furthermore, they add to the evidence suggesting that the verbal domain is a relative strength in autism while processing emotional information in comparison with non-verbal cues (Downs & Smith, 2004; Egan, Brown, Goonan, Goonan, & Celano, 1998; Fink et al., 2014; Loveland et al., 1997). To be clear, the wide variability in the behavioral responses in the ASD group, particularly for the incongruent judgments in the negative and neutral conditions, suggest that there may be phenotypic differences within ASD for both emotional valence and/or task difficulty.

Increased task-related activation in TOM network in ASD

During the EIT, participants listened to short stories describing a protagonist's internal state, be it emotional or physical. Several cognitive processes are important in making a correct inference. These include (but are not limited to) semantic knowledge, to accurately comprehend the words; empathy/mentalizing abilities, to understand how a person would feel given the situation described, and—for the emotional conditions—emotional awareness related to the context. Furthermore, all

of these processes are contingent upon the neural mechanisms needed for memory. Initial predictions were that autistic individuals would show less task-related activation in social-affective regions for emotional scenarios along with relatively more activations in brain areas associated with language. However, the results do not support these predictions, but in fact show the opposite trend. While listening to scenarios, the autism group showed enhanced BOLD activity relative to the control group in the emotional conditions, in two regions associated with ToM processing (rTPJ and pCC). Regions associated with narrative processing (NARR ROIs, not intersecting with TOM ROIs) failed to show differential activation between groups. One explanation for this may be that increases in task difficulty are associated with greater activations in relevant brain regions (Durston, Thomas, Worden, Yang, & Casey, 2002; Tamm, Menon, & Reiss, 2002). If this is the case, the demands of making affective inferences may be more burdensome for ASD relative to NT individuals. Past studies investigating right temporal involvement during mentalizing offer inconsistent results; for example, two language-based studies show the same pattern as the present study (Mason et al., 2008; Wang et al., 2006), while two others present a lack of differentiation (Castelli, Frith, Happé, & Frith, 2002; Lombardo, Chakrabarti, Bullmore, & Baron-Cohen, 2011). Wang et al. (2006) show similar increases for ASD in bTPJ (as well as mPFC) during irony comprehension, and suggest increases in ToM regions are due to more effortful processing during a task that explicitly requires attention to social cues. Mason et al. (2008) also show increases in right posterior temporal regions while reading sentences (intentional, emotional, and physical state), arguing that this may be due to “spillover” effects to

right language areas from their LH homologues as the autistic participants fail to differentiate between experimental and control conditions. In contrast, others have shown reduced differentiation between mentalizing and control conditions in rTPJ. For example, one paradigm used animated shapes depicting three different patterns of movement: goal-directed, movement with intention, or random (Castelli et al., 2002). While viewing animations with intentional movement, the control group showed differential activation in bTPJ (as well as mPFC, bSTS and baSTS), whereas the ASD group had relative decreases in all regions. Another investigation used lexical stimuli that varied by ‘self ‘or ‘other’ and ‘mentalizing’ or ‘physical’ judgments, and while controls showed increased activation in rTPJ for mentalizing, ASD failed to show the same (Lombardo et al., 2011). As all conditions of EIT stories require inferring the state of the protagonists, and our results show both significant between-group and with-in group differences in rTPJ, these increases may be due to the increased demands required both by inferring complex language and, more importantly, by the implied emotional valence.

The heightened activity in the precuneus for ASD relative to controls in response to the emotional scenarios may also be attributed to more effortful processing, as this region has a central role in a number of integrated tasks (see Cavanna & Trimble, 2006 for review), including visual-spatial imagery (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Knauff, Mulack, Kassubek, Salih, & Greenlee, 2002), self-processing (Blakemore, Den Ouden, Choudhury, & Frith, 2007; Den Ouden, Frith, Frith, & Blakemore, 2005; Kircher et al., 2002; Schacter, Addis, & Buckner, 2007), and episodic memory retrieval (Fletcher et al.,

1995; Gallagher et al., 2000; Lundstrom et al., 2003; Wagner, Shannon, Kahn, & Buckner, 2005). Episodic memories are a subdivision of “declarative” or “explicit” memories, which allow for recall of personal events (as opposed to general knowledge, or semantic memory) (Squire, 2009; Tulving et al., 1994). In autism, one study showed a similar pattern to the current research, wherein the autism group had increased differential activation in precuneus while matching emotional faces to words relative to controls, despite a lack of behavioral differences (Wang et al., 2004). By contrast, other investigations show the opposite pattern (Kennedy et al., 2006; Martineau, Andersson, Barthélémy, Cottier, & Destrieux, 2010). For example, decreased precuneus activity was shown in ASD versus controls while observing facial expressions compared to mimicking them (Martineau et al., 2010), and Kennedy et al. (2006) showed that autistic individuals failed to show a “deactivation” in precuneus during a resting-state scan versus task, whereas the control group displayed this effect. A recent meta-analysis showed that ASD participants have “robust” grey matter decreases in bilateral precuneus compared to controls, and that this volume decrease is statistically higher in right precuneus in adults with ASD relative to teens (Via, Radua, Cardoner, Happé, & Mataix-Cols, 2011). Thus, the age and/or precuneus volume (right and left independently), may have a differential effect on neural activations across a variety of tasks in autism.

The group with autism also displayed enhanced activity in subcortical areas important for general and emotional memories, for example the hippocampus (LaBar & Cabeza, 2006). Past studies have shown an overlap between network for ToM and autobiographical memory [STS, aSTS, lateral IFG (angular gyrus) pCC, dmPFC,

vmPFC, IFG, and amygdala] (Rabin, Gilboa, Stuss, Mar, & Rosenbaum, 2010; Spreng & Grady, 2009). Furthermore, while not correlated with one another, the hippocampus and rTPJ are functionally correlated with this network (Spreng & Mar, 2012). Spreng & Mar (2012) propose that the overlap between these regions supports the integration of personal information with interpersonal information, thus facilitating personal experiences to inform social knowledge. Similarly, Schacter, Addis, & Buckner (2007) put forward the concept of the "prospective brain," wherein structures important for past memories, envisioning the future and mental simulation (mPFC, precuneus, lateral temporal cortex, and medial temporal lobe) are functionally related to one another and also to the hippocampal formation. In this model, memory contributes to one's ability to simulate—or conceive—future events, and similarly to understand others' minds (ToM). Behavioral evidence shows memory impairments for emotional words and sentences in autism (Beversdorf et al., 1998; Gaigg & Bowler, 2009a, 2008), and also for emotional experiences (Losh & Capps, 2006). As such, emotional memory deficiencies may also contribute to increased neural activations in mentalizing regions in autism.

Lastly, the heightened response observed in ToM regions for ASD may also be associated with the overlap between the ToM network and regions shown to be connected during the brain's "resting state," or the default mode network (DMN), i.e., mPFC, pCC, and angular gyrus/TPJ (Buckner, Andrews-Hanna, & Schacter, 2008; Raichle et al., 2001). In autism, there is evidence of reduced connectivity in associated DMN regions along with aberrant activations within the network (Assaf et al., 2010; Cherkassky, Kana, Keller, & Just, 2006; Kennedy et al., 2006; Monk et al.,

2009). Together, the present findings suggest that in autism, language-related emotional information is processed differently from neutral stimuli in “mentalizing” brain regions, and enhanced neural activations in these areas may suggest increased task-related difficulty.

Enhanced neural response to emotion in ASD

When processing individual emotions, both groups revealed significantly more neural activity in response to emotional stories relative to neutral in rTPJ, mPFC and precuneus, and additionally in dmPFC in ASD. Furthermore, in lTPJ and bSTS the same pattern emerged, but with non-significant differences. Emotion research in neurotypical individuals shows that regions associated with social-affective processing respond to emotional linguistic stimuli, including: the rostral aCC (Whalen et al., 1998), PFC (Hynes et al., 2006; Maratos, Dolan, Morris, Henson, & Rugg, 2001), and bilateral amygdala (Ferstl, Rinck, & Von Cramon, 2005; Isenberg et al., 1999; Kiehl et al., 2001; Strange, Henson, Friston, & Dolan, 2000). Past research is mixed regarding neural response to emotion in ASD. For example, in studies of facial recognition (see Harms et al., 2010 for review), some studies show a *reduced* response (particularly in amygdala and prefrontal regions) to emotion in faces (Ashwin et al., 2007; Critchley et al., 2000; Piggot et al., 2004; Wang et al., 2006), while others indicate intact abilities (Adolphs et al., 2001; Hall, Szechtman, & Nahmias, 2003; Loveland, Steinberg, Pearson, Mansour, & Reddoch, 2008; Neumann, Spezio, Piven, & Adolphs, 2006; Ogai et al., 2003; Rutherford & Towns, 2008). For emotional prosody, reduced responses are shown in ASD (Tesink et al., 2009; Wang et al., 2006). Results from this cohort are the first to show that autistic

individuals are able to differentiate emotional from neutral affect in verbal scenarios that lack explicit emotional words and prosody.

Another novel finding is that autistic individuals showed task-related differentiation between the effect of POS and NEG emotional valence, as illustrated in Figure 11. While it is unwise to draw conclusions from a limited sample, there is a delineation between regions where POS evoked higher response than NEG in medial structures (mPFC, amygdala and precuneus), and NEG > POS in bilateral temporal regions (TPJ and STS). These responses follow the same pattern as the results from NEG > POS and POS > NEG in Study 1 (Figure 7). Research in neurotypical individuals shows that medial frontal regions are associated with social cognition and emotion (Adolphs, 2003; Adolphs, 2003b), and negative emotions often are associated with more medial- and dorsal medial PFC (Etkin, Egner, & Kalisch, 2011; Lamm et al., 2011), while positive valence relates to more to vmPFC (Wager et al., 2008). A recent meta-analysis shows this same effect, and suggests that the dmPFC is responsive to negative feedback and cognition, while the vmPFC is associated with positive feedback and social-affective acceptance (Crone, 2014). While the current results point to differential activation patterns in for positive and negative stimuli in autism, further research will be needed to investigate the effect of valence in medial frontal areas in ASD.

ASD traits predict decreased activation in amygdala and mPFC

For the independently selected ROI, amygdala and mPFC were significantly correlated with symptom severity in the autism group for three social-affective measures. However, the pattern of activation seen in other analyses were reversed.

That is, greater autistic traits were positively correlated with *less* neural activity in these two regions. For the Empathy Quotient (EQ, Figure 14: A2) those with the most impairment (low scores) had comparatively less amygdala activity, and also less activation in mPFC (Figure 14: A3). For the Reading the Mind in the Eyes test—which also evaluates empathy—lower abilities (low scores) correlated with decreases in amygdala activations (Figure 14: C2). Both regions were also significantly correlated with autistic symptoms expressed in the Autism Quotient index (AQ), where greater symptomatology (higher scores) was associated with reduced neural response in both amygdala and mPFC (Figure 14: B2, B3). These significant correlations occurred in the BOLD responses to the POS condition.

Not surprisingly, brain regions associated with empathizing in the neurotypical population vary depending on the nature of the task and stimuli, and past studies have shown differential effects between cognitive- and emotional empathy. For example, making empathic judgments during verbal tasks is associated with elevations in superior- and inferior FG, middle temporal gyri and precuneus (Farrow et al., 2001). Another language-based study compared emotionally-charged moral and non-moral judgments (Moll, de Oliveira-Souza, Bramati, & Grafman, 2002). During moral judgments, enhanced activations were shown in medial orbito-frontal regions, laSTS and lSTS. However, the *emotional* non-moral condition activated amygdala, orbital frontal gyrus, and lingual gyri. Emotional regions (amygdala and aCC) also showed significant signal increases while participants imitated emotional facial expressions, relative to viewing the same (Carr et al., 2003). Empathy for negative events, like watching a loved one experience physical or emotional pain, is associated

with aCC and insula (Lamm et al., 2011; Singer et al., 2004). In a direct comparison of ToM and empathy, cartoons showing mentalizing elicited lateral orbito-frontal regions, mPFC, STG and cuneus, while those describing empathy evoked activations in additional “emotional” regions: paracingulate, aCC, pCC and amygdala (Völlm et al., 2006); this overlap between ToM and emotional networks has also been shown during emotional prosody judgments (Hervé, Razafimandimby, Jobard, & Tzourio-Mazoyer, 2013).

Summarily, the significant increases observed in brain-behavior relationships in mPFC and amygdala for empathy measures may suggest a more “typical” activation pattern for autistic individuals during emotional empathy. The fact that these relationships were significant only in the POS contrast—which behavioral scores suggest were easiest to infer—adds some evidence to this proposition.

Right STS does not modulate according to ASD symptomatology

For the NT group, right STS showed significant increases related to greater social skills, whereas the ASD group showed no effect in this region. A large body of literature on neurotypical individuals has associated rSTS with aspects of social cognition (see Redcay, 2007 for review), including processing language (Kriegstein & Giraud, 2004; Willems, Özyürek, & Hagoort, 2009), facial expressions (Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001), eye gaze (Pelphrey, Viola, & McCarthy, 2004), body movements/gestures (Kircher et al., 2009; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004), and intentions (Pelphrey, Morris, & McCarthy, 2004). Research in autism suggests impaired activation in rSTS in response to social stimuli (see Pelphrey, Shultz, Hudac, & Vander Wyk, 2012; Redcay, 2008; Zilbovicius et al.,

2006 for reviews). Specifically, whereas neural activations in neurotypical participants differentiate between social and non-social stimuli in this region, autistic individuals fail to show the same pattern, e.g., while watching goal-directed and mental state animations (Castelli et al., 2002), listening to voices versus other sounds (Gervais et al., 2004), perceiving intentional gaze shifts (Pelphrey, Morris, & McCarthy, 2005). Furthermore, there is evidence of increased specialization of rSTS for social stimuli with age (Blakemore et al., 2007; Redcay, 2008). A challenge for future research will be to investigate the differential effects of the brain-behavior relationships shown in the present study.

Cognitive reappraisal regions activated during response epoch in ASD

Results related to neural activations for the response epoch include a significant interaction effect for NegCon (NT > ASD) and NegIncon (ASD > NT) in superior mPFC, aCC, and right angular gyrus. With the exception of aCC, these results fail to support the predicted regions associated with cognitive control/error monitoring (dlPFC, paCC, rIPL, pCC, precuneus, insula; Botvinick et al., 2001). However, these results are suggestive of the behavioral responses, where the autism group displayed greatest difficulty (via slower and less accurate responses) in both NegIncon and NeutIncon. The brain regions where the interaction elicited significant activations are associated with emotion and ToM/social processing (rostral aCC, dmPFC, mPFC, and lpSTS), where dmPFC is highly associated with negative valence (Lamm et al., 2011; Singer et al., 2004).

In studies of cognitive control of emotion (see Ochsner & Gross, 2005 for review; Ochsner et al., 2009), “controlled regulation” describes cognitive change to

regulate an ongoing emotional response. “Reappraisal” is one type of controlled regulation, involving the reinterpretation of an emotional stimuli to change one’s emotional response to the same (Gross, 1998), and medial prefrontal and aCC regions are shown to be differentially involved during reappraisal of negative emotion depending on the stimuli and nature of the task (Ochsner & Gross, 2005). Cognitive reappraisal strategies were key during the incongruent trials of the EIT. For example, for this negative scenario: “*The man's boss made him work late, so he hit traffic on the way to the airport. When he finally pulled off onto the airport exit, he was out of gas. He missed his flight*” the incongruent response is: “*He felt love.*” And in autism, the enhanced neural response mPFC and aCC during such negative incongruent trials possibly suggests more effortful cognitive reappraisal. The fact that the autism group showed similar behavioral difficulties in NeutIncon conditions, but that the same condition failed to show a group x condition interaction neural effect, may be due to the lack of emotional information in the neutral condition. More research is needed to determine the differential effect that valence has on cognitive control in autism.

Conclusion and future directions

The research presented herein represent the first cohort of a larger data collection effort that is underway; the intention is to add five to ten more participants per group to increase statistical power. This is crucial given the heterogeneity in autism and the fact that autistic traits occur on a continuum in the neurotypical population. Nevertheless, the results of the present study are compelling, and suggest that autistic individuals are able to correctly identify others’ feelings from language that lacks overt prosodic elements or emotionally-charged words. Furthermore, like

neurotypical individuals, their neural activations show enhanced response to conditions of valence (positive and negative) compared to neutral in areas associated with mentalizing. However, in contrast to controls, the autism group showed overall greater brain activations, possibly suggesting that for them, the task is more effortful. As decreased functional connectivity has been associated with increases in activation, performing a functional connectivity analysis will be an important next step in determining the relationship between regions where enhanced activation was observed. Increasing the sample size will also allow for more detailed between-group comparisons of possible interactions between the conditions of valence and brain activity. Another consideration will be to control for individual variance, both in behavioral analyses and in terms of neural activity. Variability in cognitive performance (accuracy and RT on EIT task), social abilities, grey matter volume differences and the use of psychostimulants during the fMRI scan[5] will be important factors to explore. The question of differences in the neurotypical samples between Study 1 and Study 2 should also be addressed, especially if these differences are exacerbated with increased sample size. In terms of ROI analyses, it may be fruitful to perform a modified analysis by extracting parameter estimates from each participant individually for the scenario epoch, as opposed to the group average approach employed in Study 2. Likewise, an FIR (Finite Impulse Response) analysis would reveal possible differences between groups in the temporal unfolding of the haemodynamic response during the extensive story epochs. An item analysis—investigating the effects of individual emotions—would also add to the literature

[5] Some ASD participants would have been unable to participate in the brain scan without medication.

regarding emotional understandings in autism. Furthermore, an item-analysis may also help determine the important question of whether the EIT scenarios truly evoke *emotional* inferences (as suggested herein), or rather invoke more general theory of mind processes, not specific to emotion.

Regarding the theoretical models presented in the first Chapter, this research lends limited support to the idea that "weak central coherence" (WCC) or difficulty making global inferences (Happé & Frith, 2006) may be at the root of understanding emotions in the context of language for autistic individuals. As a whole, the autistic participants were able to make correct judgments in about 95% of the congruent probes, contradicting other findings showing impairments in understanding inferential language (Dennis et al., 2001; López & Leekam, 2003). However, their accuracy judgments showed that they had greater difficulties with the incongruent items, especially for negative and neutral scenarios (where accuracy was ~87% for both). Difficulties with "mixed messages"—as represented by the incongruent items—may be reflected in real life social situations, where autistic individuals often struggle to quickly and successfully interpret inconsistent verbal information that includes innuendos, sarcasm and humor. This interpretation should be used with caution, however, as the same pattern was not observed for incongruent positive items.

In terms of the second theory presented—impairment of complex processing—the findings provide mixed support. Specifically, the behavioral findings fail support the notion of weakness in complex language and complex memory in autism (Minshew & Goldstein, 1998). However, the differential neural results between the autistic group and neurotypicals may offer support for this theory

inasmuch as this model was refined to predict that autism is a disorder of neural connectivity (Minshew & Williams, 2007). Functional connectivity analyses (to be calculated on a larger sample) will help clarify this stance.

The findings of this research are most consistent with the proposal that the social deficits in autism result from weaknesses in mentalizing, or ToM (Frith & Frith, 1999; Frith & Frith, 2003; Frith, 2001). Even though the autistic individuals showed abilities in task performance, their relative increases in neural activations relative to the neurotypical group, especially in regions shown to be associated with mentalizing, suggest impairments in understanding what others are thinking or feeling. The fact that there was more differentiation between the emotional conditions than the neutral condition in these regions suggests that emotional valence may require additional resources. As mentioned above, future analyses will be useful in determining whether the EIT taps emotional processes or more general understandings of what others are thinking.

Overall, these findings represent an important first step toward uncovering relative social-affective *abilities* in the language context in autistic individuals, despite irregular neural responses. The experimental approach the Emotional Inference Task provides greater precision with respect to deriving implicit emotional states and the underlying neural correlates. Moreover, such tasks have not been done in individuals with ASD, particularly in the context of fMRI. The findings from this and future work may be used to design effective intervention strategies and therapeutic practices for autistic individuals and their loved ones, for example by focusing more heavily on increasing language proficiency and using lexical

information as a crutch or tool in place of facial expressions which have a higher degree of variability and nuance. Successful remediation often employs areas of relative skill, and uses these to positively influence deficits.

Appendix A: Stimuli, Van Lanker et al., (1991); Hobson and Lee (1989)

Table 1.

Stimuli from Van Lanker et al. (1991) and Hobson and Lee (1989)

Van Lanker et al. (1991)			Hobson and Lee (1989)		
Emotional adjectives	Neutral adjectives	Object nouns	Emotional items	Abstract items	Social-related items
hurt	hot	wagon	horror	time	accident
disappointed	round	bicycle	delighted	sharing	sharing
scared	messy	flower	disagreement	horror	dentist
sad	big	picture	surprise	delivering	delivering
happy	old	carrot	greeting	delighted	tugging
mean	furry	glass	snarling	disagreement	teacher
furious	heavy	bed	embracing	pair	disagreement
lively	gentle	eye		surprise	waiter
guilty	thirsty	drum		greeting	greeting
surprised	clean	bus		snarling	entertainer
lazy	square	camera		isolation	isolation
angry	broken	brush		predatory	applauding
sleepy	dirty	piano		triplet	predatory
tired	fat	book		adjustable	stunt
loving	soft	hand		parallel	lecturing
hurt	hot	wagon		catastrophe	departing
disappointed	round	bicycle		departing	embracing
scared	messy	flower		portable	accident
sad	big	picture		coniferous	sharing
happy	old	carrot		filtration	dentist
mean	furry	glass		tranquil	

Appendix B: Pilot study

As novel stimuli were generated for this research, a pilot study was conducted prior to conducting the fMRI studies to generate norms and determine the most suitable items.

Sentence construction

The initial corpus was composed of 36 short scenarios with implied negative emotional context, 36 with positive context, and 36 story passages describing the protagonist's physical state (see Table 1 for examples). The sentences were constructed such that the information related to the feeling- or physical state appeared as close to the beginning as possible, and the same state was inferred throughout the story. All sentences were designed to be consistent with a target emotional- or physical state fitting the response, "He/she felt *xxx*." Target emotion words around which the positive and negative target sentences were created were selected Mind Reading software (Baron-Cohen, Wheelwright, & Hill, 2004), a program that includes over 400 emotion words; target words chosen were rated as familiar to 95% of 15-16 year olds (Baron-Cohen, Golan, Wheelwright, Granader, & Hill, 2010). Words forming the basis of the neutral target sentences related to a bodily state or physical condition and lacking an emotional dimension in the sentential context. Table 2 presents the target words for all scenarios.

Sentence production

Passages were recorded by an adult female using Praat recording software (pitch range 100-500 Hz, sampling frequency 44100 Hz, mono signal) (Boersma &

Weenink, 2012). A natural tone of voice was used, lacking prosody and affective intonations that would be consistent with the emotion portrayed (or lack thereof). Initial recordings were normalized for intensity by calculating the average of all files (72.45 db total, range 67.81 to 77.15) and scaling all recordings to this average. To verify the absence of prosodic cues, an acoustic analysis was conducted to evaluate the utterances on the activation dimension (high vs. low energy) using PRAAT software (Boersma & Weenink, 2004). Particular attention was paid to F0, the main parameter reflecting emotion in prosody, with negative emotions characterized by a low, monotonous F0 pattern and positive emotions by higher, more wide-ranging F0 (Bänziger & Scherer, 2005; Scherer, 1986). Single factor analysis of variance failed to reveal differences between conditions for either mean F0 (ANOVA; $F(2,69) = .68$, $p = > .05$) or F0 range (ANOVA; $F(2,69) = 1.63$, $p = > .05$). The stories had an average duration of 11.02 sec (range 9.74-11.74 sec).

Table 1.

Sample scenarios for pilot study

Condition	Scenario
Negative	The woman could not get over the idea that her ex-boyfriend did not want to be with her anymore. Hearing that he was dating someone new made the situation even worse.
Positive	The young man had waited so long for his favorite band to come to town that he could hardly sleep the night before the concert. He planned to arrive early to get autographs.
PhyState	After the race, the jockey was covered head to toe, and he couldn't see through his goggles. Days of rain had saturated the track, so the horses kicked up great clods as they ran.

Note. A total of 108 sentences were constructed, 36 each negative-, positive- and physical state. Emotional- or physical state was implied.

Table 2.

Target words for each condition in emotional inference task

Negative		Positive		Physical State	
Feeling	Scenarios	Feeling	Scenarios	Feeling	Scenarios
Angry	3	Excited	4	Dirty	6
Disappointed	3	Happy	2	Hot	3
Disgust	3	Love	5	Wet	3
Frustrated	3	Overjoyed	3	Tired	2
Jealous	3	Proud	3	Hungry	2
Sad	3	Relieved	3	Cold	3
Scared	3	Romantic	2	Sore	5
Upset	3	Welcomed	2		

Note. Positive and negative scenarios were created around emotionally valent target words chosen from the Mind Reading software program (Baron-Cohen et al., 2003). Physical state scenarios were designed to project a bodily state or physical condition, but not an emotional dimension in the sentential context. The numbers under "Scenarios" reflects the final corpus.

<u>Sentence selection</u>

Nineteen typically developing adults (11 F; 18.1-22.5 years of age) recruited from the University of Maryland performed a cloze task procedure to assess the precision of the contexts in evoking particular emotional states. Additionally, stories were rated for valence and familiarity. For the task, participants were seated in front of a computer monitor on which a horizontal scale was displayed: -3 (negative) to +3 (positive), with 0 being the anchor for neutral. As they listened to each scenario using headphones, subjects were asked to move the computer mouse far to the left if they felt it was highly negative or similarly to the right for highly positive. For less intense feelings, they were asked to keep the mouse closer to the midline (0). Participants were asked to commence the movement of the mouse at the time when they identified the valence of the story, and after listening to the story, they typed a word that best fit the feelings of the protagonist. Finally, they judged the likelihood of the scenario by

entering a number from 1 (*not at all likely to* happen) to 7 (*very likely to happen*) in response to: “Could you imagine this actually happening to you or someone close to you?” Participants could choose to hear the story again if they desired. Each subject responded to all 108 scenarios.

The criteria used for sentence selection were a) positive and negative scenarios were deemed appropriate if they received 100% agreement from all participants (target word or a synonym), b) physical state stories were deemed accurate if response was consistent with the physical state *or* a neutral emotion was supplied, e.g., "satisfied." Furthermore, among those stories meeting the consistency criteria, those judged to have highest (for positive), lowest (for negative) and most neutral (for physical state) valence ratings were selected. Valence ratings were collected on a scale of -3 to +3, -3 being most negative and +3 most positive. The average valence for negative stories = -2.48, for positive stories = 2.52, and for neutral stories = -1.80 (see Table 3 for complete results). In total, 72 sentences were chosen, 24 in each condition. For the fMRI paradigm, congruent and incongruent response conditions were created for each of the scenarios in the form of a true-false statement, for example, “She felt happy.” The corpus of scenarios and their incongruent T/F response choices are in Appendix C.

Table 3.

Averages for emotional inference task scenario stimuli

Condition	Duration (msec)	Percent consistency	Valence	Familiarity	Response start time (msec)	Percent male
Negative	1107	100.00	-2.49	4.40	7434	41.70
Positive	1102	100.00	2.52	5.25	7721	50.00
Neutral	1112	89.71	-1.80	4.47	9432	67.00
Total	1104	96.57		4.71	8193	52.70

Note. Parameters for final scenario stimuli chosen from pilot study, including a) average duration, b) consistency of responses from the cloze task, c) average valence (scale: -3 to +3), d) familiarity (scale: 1 to 7), e) average response time, and f) percent of stories with male protagonists.

<u>Stimuli norming</u>

To determine consistency between conditions (Table 4) in the final stimuli were submitted to Coh-Metrix version 3.0, an on-line database that calculates text coherence on a wide range of measures (McNamara, Louwerse, Cai, & Graesser, 2005). For stories, means and standard deviations were calculated for five measures: *number of sentences*, *words per sentence*, *narrativity*, *syntactic simplicity*, and *words before main verb*. The first two measures are self-explanatory, and did not differ when tested by a single factor analysis of variance (ANOVA; $F(2,69) = 2.69$, $p < .05$) for number of sentences or (ANOVA; $F(2,69) = 1.90$, $p < .05$) for words per sentence. *Narrativity* is a measure closely affiliated with every day oral conversation; this measure is highly affiliated with word familiarity, world knowledge, and oral language. Non-narrative, unfamiliar texts lie at the other end of the spectrum. Scenarios in each condition did not differ in terms of *narrativity* tested by a single

factor analysis of variance (ANOVA; $F(2,69) = 1.52$, $p < .05$) for z-scores and (ANOVA; $F(2,69) = 1.36$, $p < .05$) for percentile.

Table 4.

Norming results for story stimuli

	Valence		
	Positive	Negative	Neutral
	M (SD)	M (SD)	M (SD)
Sentences			
Number sentences	2.04 (.62)	2.33 (.56)	2.0 (.42)
Words per sentence	33.13 (2.85)	33.46 (2.78)	31.96 (2.76)
Narrativity	64.83 (37.94)	73.82 (31.24)	57.04 (36.19)
Syntactic simplicity	17.56 (21.87)	30.44 (31.37)	32.98 (23.35)
Words before main verb	5.90 (5.98)	4.01 (2.71)	4.55 (1.90)
Content words			
Frequency	2.19 (.24)	2.26 (.27)	2.18 (.28)
Age of acquisition	276.62 (51.20)	286.88 (67.24)	280.80 (61.05)
Familiarity	583.76 (12.61)	583.89 (12.15)	580.62 (12.65)
Concreteness	443.52* (39.54)	425.26* (46.81)	463.63* (36.37)
Meaningfulness	472.45* (24.31)	447.75* (28.63)	453.82* (17.49)
Imagability	479.74* (32.50)	453.79* (42.93)	488.95* (34.39)

Note. Means and standard deviations (in parentheses) calculated using Coh-Metrix version 3.0 (McNamara et al., 2005). Narrativity = highly associated with word familiarity, world knowledge, and oral language. Syntactic simplicity = the degree to which the sentences in the text contain fewer words and use familiar syntactic structures. Words before main verb = mean number of words before the main verb of the main clause in sentence; good index of working memory load. Frequency = average word frequency for content words (CELEX). Age of acquisition compiled by Gilhooly and Logie (1980) higher scores = word is learned later. Familiarity = rating (on a 7-point scale) of how familiar a word seems to an adult. Concreteness = index of how concrete or non-abstract a word is. Meaningfulness from Toglia and Battig (1978), higher scores = word is closely related to others. Imagability = how easy it is to construct a mental image of the word.
$^*p < .05$

Syntactic simplicity reflects the degree to which the sentences contain fewer words and use simple, familiar syntactic structures (as opposed to complex structures with more words). Scenarios did not differ in terms of syntactic simplicity tested by a single factor analysis of variance (ANOVA; $F(2,69) = 1.81$, $p < .05$) for z-scores and (ANOVA; $F(2,69) = 1.48$, $p < .05$) for percentile. *Words before main verb* calculates the mean number of words before the main verb of the main clause in sentences; this

measure provides a good index of working memory load. No differences were found when tested by a single factor analysis of variance (ANOVA; $F(2,69) = 1.46$, $p <$ .05).

Content words in the scenarios were also submitted for analysis on six measures: *frequency*, *age of acquisition*, *familiarity*, *concreteness*, *meaningfulness* and *imagability* (Table 4). Single factor analysis of variance failed to reveal differences between conditions for *frequency* (ANOVA; $F(2,69) = .54$, $p < .05$), *age of acquisition* (ANOVA; $F(2,69) = .84$, $p < .05$), or *familiarity* (ANOVA; $F(2,69) =$ .54, $p < .05$). Differences were revealed in the remaining measures, however. Content words differed significantly in terms of *concreteness* (a measure of how "non-abstract" a word is) tested by a single factor analysis of variance (ANOVA; $F(2,61.0) = 6.12$, $p < .05$). Planned comparisons revealed that content words in neutral stories were significantly more concrete those in negative stories $t(69) = 3.23$, $p < .05$ and emotional (positive and negative) stories together $t(69) = 2.84$, $p < .05$. Content words also differed significantly in terms of *meaningfulness* (ANOVA; $F(2,69) = 6.18$, $p < .05$. Planned comparisons revealed that content words in positive stories were significantly more meaningful those in negative stories $t(45.3) = 3.04$, $p < .05$, neutral stories $t(40.9) = 2.81$, $p < .05$, and negative and neutral stories together $t(42.7) = 3.34$, $p < .05$. Lastly, content words differed significantly in terms of *imagability* (index of how easy it is to create a mental image of the word) (ANOVA; $F(2,69) = 5.86$, $p < .05$). Planned comparisons revealed that content words in negative stories scored significantly lower in terms of *imagability* than those in neutral stories $t(69) = 3.3$, $p < .05$, and positive stories $t(69) = 2.44$, $p < .05$.

Additionally, emotional stories combined had lower *imagability* ratings than neutral stories $t(69) = 2.41$, $p < .05$.

Content words from the target probes were similarly analyzed for consistency on five measures: *length*, *frequency*, *familiarity*, *concreteness* and *imagability* (Table 5). Single factor analysis of variance failed to reveal differences between conditions for *length* (ANOVA; $F(2,69) = 3.47$, $p < .05$), *frequency* (ANOVA; $F(2,69) = .82$, $p < .05$), *familiarity* (ANOVA; $F(2,69) = 3.0$, $p < .05$), *concreteness* (ANOVA; $F(2,69) = 1.82$, $p < .05$), or *imagability* (ANOVA; $F(2,69) = 2.99$, $p < .05$).

Table 5.

Norming results for content words in target probe

	Valence		
	Positive	Negative	Neutral
	M (SD)	M (SD)	M (SD)
Length	6.75 (1.83)	6.88 (2.90)	4.26 (1.11)
Frequency	1.47 (.70)	1.06 (.61)	1.36 (.69)
Familiarity	292.38 (313.89)	413.0 (256.61)	596.0 (29.08)
Concreteness	167.88 (179.97)	169.13 (182.94)	340.43 (233.76)
Imagability	248.0 (267.82)	324.38 (204.55)	497.71 (42.03)

Note. Means and standard deviations (in parentheses) calculated using Coh-Metrix version 3.0 (McNamara et al., 2005). Frequency = average word frequency for content words (CELEX). Age of acquisition compiled by Gilhooly & Logie (1980) higher scores = word is learned later. Familiarity = rating (on a 7-point scale) of how familiar a word seems to an adult. Concreteness = index of how concrete or non-abstract a word is. Meaningfulness from Toglia & Battig (1978), higher scores = word is closely related to others. Imagability = how easy it is to construct a mental image of the word.
*p < .05

Appendix C: Complete stimuli for Emotional Inference Task

Condition/No.	Scenario	Congruent Target	Incongruent Target
Neg1	The woman could not get over the idea that her ex-boyfriend did not want to be with her anymore. Hearing that he was dating someone new made the situation even worse.	jealous	overjoyed
Neg2	The girl tried hard to smile when only her sister was accepted to Yale. The twins were both top students, and had both applied to many of the same prestigious schools.	disappointed	romantic
Neg3	The girl's name was not among those who made the cheerleading squad. All of her friends were chosen, as well as two other girls who were not very agile and had messed up on their routines.	disappointed	welcomed
Neg4	No one visited the woman when she was hospitalized with pneumonia. The phone didn't ring, and she received no flowers or cards. During visiting hours her room was silent.	sad	romantic
Neg5	As usual, the girl was the last one picked for the team. She was left standing alone, as the losing captain waved her over. Even the skinny new kid was picked before she was.	sad	loved
Neg6	The babysitter took the toddler to the park to play, and when she turned around he was gone. She quickly searched the playground, and then raced across the field to search the woods.	scared	relieved
Neg7	Just as the man raised the forkful of fried rice to his mouth, he noticed something moving on his plate. He dropped his fork when the black cockroach scurried out of his food.	disgust	love
Neg8	The reporter arrived at the scene of the overturned bus on Route 1. He saw people moaning and blood all over the road. His stomach turned as medics covered a victim.	disgust	loving
Neg9	The computer screen was still black, even after the man had spent two hours on the phone with the service department, restored the factory settings, and installed a new hard drive.	frustrated	excited
Neg10	When the woman got her silk sweater back from her roommate, it reeked of cigarette smoke and had underarm stains. Even after paying to have it dry-cleaned, it wasn’t the same.	angry	proud
Neg11	Because she had detention, the girl missed the pool party. The whole class was there, including her friends who also skipped class. The girl sat in the classroom glaring at the proctor.	angry	relieved
Neg12	The man's boss made him work late, so he hit traffic on the way to the airport. When he finally pulled off onto the airport exit, he was out of gas. He missed his flight.	frustrated	love

Condition/No.	Scenario	Congruent Target	Incongruent Target
Neg13	His grandfather's death came suddenly. When the boy heard the news, he remembered the old man's deep laugh, his gentle hands and the chair that would now be empty on holidays.	sad	excited
Neg14	Her boyfriend unexpectedly broke up with her, without even making a phone call. He simply sent a text message to her phone, saying that it was over, and not to contact him anymore.	upset	excited
Neg15	The student had worked for days on his essay when his computer crashed. He had not made a back-up copy, and it was due in two days. Without this he would fail the class.	frustrated	happy
Neg16	It snowed so hard on her wedding day that the couple could not make it to the church. Many guests were unable to come, and the caterers cancelled. Months of planning were ruined.	disappointed	proud
Neg17	The boy threw down his backpack, stomped down the hallway, snarled at his sister then slammed his bedroom door. When his mother knocked and asked him to come out, he demanded to be left alone.	angry	relieved
Neg18	The girl saw that her new bike was gone when she returned to the bike rack. She had locked it up, but found that her lock was left dangling. It was a birthday present, and she had only had it for three months.	upset	love
Neg19	Late at night, the girl woke up when she heard scratching at her window. Soon after she heard shuffling sounds, and the neighbor's dog barking. Then, the door handle jiggled.	scared	proud
Neg20	The toilet in the public restroom had overflowed all over the floor. When the unsuspecting woman stepped into the stall, she was met with an indescribable sight and stench that caused her to back away.	disgust	overjoyed
Neg21	The elevator came to a violent stop and the lights went out. As the man felt his way along the wall, hoping to find the emergency call button, the elevator began jerking again.	scared	happy
Neg22	The woman's dog had not eaten in two days, and when she came home she found him lying on his side, unable to move. She wrapped him in a blanket, and took him to the vet.	upset	excited
Neg23	The man walked into the bar and saw his girlfriend talking and laughing with three other men. She was wearing a tight dress he didn't recognize, and was openly flirting with them.	jealous	overjoyed
Neg24	The young man watched as the girl he had been talking to all evening eyed the new guy entering the gym. He was tall, handsome, and confident, and approached the girl smiling.	jealous	welcomed

Condition/No.	Scenario	Congruent Target	Incongruent Target
Pos1	At her new school, the girl's friends complimented her clothes, showed her around campus, helped her with homework when she was absent, and invited her out on weekends.	welcomed	sad
Pos2	The woman found an invitation to the state dinner at the White House in her mailbox. She quickly phoned her friends with the news, and turned her attention to buying a new gown.	overjoyed	disappointed
Pos3	The young man had waited so long for his favorite band to come to town that he could hardly sleep the night before the concert. He planned to arrive early to get autographs.	excited	disgust
Pos4	His first day on the job, the intern mounted the steps on Capitol Hill two at a time. He had wanted to be a politician, and now he pushed open the doors with a broad smile.	proud	disappointed
Pos5	The young mother held her baby gently in her arms and gazed at his small face. As he clasped his small hand around her finger, she studied each nail and his delicate skin.	loving	frustrated
Pos6	When his advisor informed him that he had had passed his exams with high marks and had enough credits to graduate, the young man left the office with his head held high.	proud	jealous
Pos7	The girl nestled into the sofa at her father’s side, and he closed his arm around her. It was one of her favorite times of the day, and she opened the book for him to read.	happy	angry
Pos8	The little boy's grandma brings him special treats when she visits, and when he goes to her house, the fresh-baked smell of his favorite cookies greets him as he opens the door.	happy	frustrated
Pos9	When he returned to work after his surgery, the man's locker was decorated with streamers and get well signs, and flowers waited on the table. His co-workers embraced him warmly.	welcomed	upset
Pos10	The woman's doctor told her she was cancer free. After battling cancer for four years, this long-awaited news meant that she could reclaim her life and think about her future.	relieved	disappointed
Pos11	The young man walked along the beach with his girlfriend, holding her hand and whispering in her ear. In the moonlight, he looked into her eyes and asked her to marry him.	romantic	angry
Pos12	The woman planned a candlelight dinner for her husband. She placed fresh-cut flowers on the table, prepared his favorite meal, and tucked a love poem under his napkin.	romantic	angry
Pos13	The young man gazed at his date and found himself thinking of a future with her. She was everything he dreamed of: smart, funny, and pretty. He smiled and squeezed her hand.	love	disgust

Condition/No.	Scenario	Congruent Target	Incongruent Target
Pos14	On her wedding day, the bride looked into her husband's eyes and told him that he would always be her one and only. Hearing the same words from him made her complete.	love	frustrated
Pos15	On their anniversary, the man told his wife that he would marry her all over again. She had made his life complete, as a supportive partner and mother to their children.	love	upset
Pos16	The young man couldn't believe his luck. His friend had gotten several tickets to the Super Bowl, and he offered one to him. He could hardly wait to see his favorite team play for the Lombardi trophy.	excited	scared
Pos17	When the teacher announced there would be no homework for the rest of the week, the girl could hardly believe it. Her afternoons and evenings would be free for her to relax, watch TV, and play with her dog.	relieved	scared
Pos18	The man won the national tournament. He held the trophy high above his head and smiled for his family and the cameras. The years and years of practice, hard work and discipline had paid off in the end.	proud	sad
Pos19	When she saw the large envelopes from Harvard and MIT in her mailbox, the young woman quickly ripped them open and read "Congratulations, welcome to the class of 2012."	overjoyed	jealous
Pos20	The woman opened the small box and found the most exquisite, glittering diamond ring. She looked into her boyfriend's damp eyes then wrapped her arms tightly around him, vowing never to let him go.	loved	disgust
Pos21	The young man had finished his exams and turned in his final paper. He walked across the quad with a spring in his step as he left campus for six weeks of relaxation.	relieved	scared
Pos22	Finally, the new release of the 'Call of Duty' video game hit the stores. The boy bought a copy, invited his friend over, ripped off the cellophane wrapper and inserted the disk.	excited	upset
Pos23	The girl's dad was finally coming home. He had been fighting in Afghanistan, but all she cared about was seeing his face in that doorway. Her heart beat rapidly as she waited.	overjoyed	jealous
Pos24	The woman boarded the plane for Australia, a place she had always hoped to visit. As an avid scuba diver, diving off the Great Barrier Reef would be like a dream come true.	excited	sad
Phys1	After the race, the jockey was covered head to toe, and he couldn't see through his goggles. Days of rain had saturated the track, so the horses kicked up great clods as they ran.	dirty	clean

Condition/No.	Scenario	Congruent Target	Incongruent Target
Phys2	Even after scrubbing her hands twice, the gardener had earth packed under her nails and smeared on her face. She had been planting bulbs in the damp soil all morning.	dirty	clean
Phys3	The drought had reduced the ranch to a barren landscape. After a day of riding, the cowboy's skin and clothing were grey-brown and his white horse was the color of the earth.	dirty	clean
Phys4	The man hadn't bathed properly or washed his clothes for the two months he had hiked the Appalachian Trail. When he emerged from the woods, he noted that people backed away from him.	filthy	clean
Phys5	Rain had turned the baseball field into a slippery mess, so when the boy slid into home base, his white uniform turned dark brown all along one side, along with his arm.	dirty	clean
Phys6	The man's skin and clothing were black with soot when he emerged from the coal mine. Under his safety helmet, his hair was matted, and he left a black trail when he walked.	filthy	clean
Phys7	The archeologist had worked all day in the sun. Her lips were cracked and her hands were red and raw. Her hat had been ineffective against the baking sun in the desert.	hot	cold
Phys8	The temperature had not gone below 100 degrees for days. The man's air conditioner was broken, and opening the windows only increased the temperature inside his apartment.	hot	cold
Phys9	It was so humid in Bangkok that the man loosened his tie and took off his jacket after the meeting. Even so, by the time he reached the hotel he had to change his clothes.	hot	cold
Phys10	It started to drizzle as the boy biked home, but the rain quickly grew stronger. By the time he got to his house, his t-shirt was see-through and his jeans were plastered to his legs.	wet	dry
Phys11	The boy had intended on washing his Golden Retriever outside with the hose, but after the dog shook vigorously, it was difficult to see who had gotten the bath.	wet	dry
Phys12	The soccer game was only half way over when it began to rain. By the time it ended, the boy's hair stuck to his head and his shoes made squishing sounds when he walked.	wet	dry
Phys13	The swimmer had been training three times per day for weeks as he prepared for the Olympic trials. After a particularly long work-out, he could hardly lift his swim bag.	tired	energetic
Phys14	The woman's legs gave away as she crossed the finish line after the long race. She had attempted to stumble over to the grass to sit down, but simply collapsed before she got there.	tired	energetic

Condition/No.	Scenario	Congruent Target	Incongruent Target
Phys15	The teenager was growing like a weed. Each day after football practice, he rummaged through the refrigerator, taking out meats, cheeses, tomatoes and lettuce to make himself a hearty sandwich.	hungry	full
Phys16	It was seven pm, and the young woman had not eaten anything since breakfast that morning. On her way home from work, she stopped at a drive through and ordered enough food for a small family.	hungry	full
Phys17	The boy had been playing in the snow all morning, without noticing the sinking temperatures. When he came in, his fingers and toes were blue, and his cheeks were bright red.	cold	hot
Phys18	Shivering in his thin t-shirt and shorts, the boy hurried home from soccer practice at the park. The temperature had dropped at least 10 degrees since he came, and snowflakes were dancing on the air.	cold	hot
Phys19	The temperature dropped to below zero when the sun went down. Shivering, he rubbed his hands together briskly. His windbreaker and cap were no match for these conditions.	cold	hot
Phys20	The old man's hands were swollen and his skin was cracked. Years of working as a stone mason had created thick callouses and he had large knuckles from arthritis.	sore	pain free
Phys21	After running the marathon, the woman could barely get out of bed, and when she did she took small, halting steps. When she went up or down stairs she took one at a time.	sore	pain free
Phys22	The old woman had difficulty moving her neck and back, and noticed increased difficulty getting out of bed in the morning. She applied heating cream to her joints.	sore	pain free
Phys23	After getting her wisdom teeth out, the girl could only eat ice cream. Slowly, she began to eat soft foods, carefully avoiding the places where her teeth had been.	sore	pain free
Phys24	After surgery to repair the torn ligament in her knee, the young woman had physical therapy. After each session, she walked slowly and gingerly to protect her knee.	sore	pain free

Appendix D: Whole brain neural results scenarios, Study 1

Table 1.

Brain activity associated with all stories, Study 1

	Left					Right				
Region label	*x*	*y*	*z*	*t*	*d*	*x*	*Y*	*z*	*t*	*d*
Frontal										
dmPFC	-8	50	34	11.17	2.91	8	56	24	6.05	1.58
	-6	56	26	6.54	1.70					
MFG	-44	4	60	9.12	2.37					
	-40	0	62	8.87	2.31					
vmPFC	-2	28	-22	10.23	2.66	2	54	-14	8.23	2.17
	-2	44	-20	9.97	2.60					
SMA	-4	4	64	9.27	2.41					
	-6	-20	66	8.74	2.28					
Precentral gyrus	-50	-4	50	10.33	2.69	56	-4	52	7.41	1.93
	-38	2	52	8.83	2.30	48	-16	68	6.34	1.65
	-36	0	48	8.53	2.22	26	-12	78	6.34	1.65
	-44	-12	40	6.56	1.71	24	-24	62	5.86	1.53
	-44	-10	66	5.92	1.54					
Paracentral lobule	-12	-38	66	8.72	2.27	8	-22	60	9.43	2.46
	-8	-38	66	7.96	2.07	4	-28	62	7.94	2.07
						10	-28	66	7.88	2.05
						12	-26	72	7.23	1.88
						12	-34	56	7.11	1.85
Insula						46	-6	18	7.09	1.85
						60	26	26	6.18	1.61
Temporal										
aSTS	-48	10	-14	16.81	4.38	50	16	-18	16.45	4.28
						58	14	-22	14.71	3.83
						42	26	-32	12.93	3.37
						48	-18	8	12.24	3.19
						34	4	-20	6.04	1.57
STS	-58	-28	10	20.00	5.21	60	-6	-2	22.75	5.92
	-62	-14	6	19.37	5.04	62	-10	2	18.76	4.88
	-60	-16	0	19.06	4.96	64	-16	6	14.84	3.86
	-46	-32	6	18.48	4.81	48	-28	8	14.29	3.72
	-56	-10	-6	18.38	4.79					
	-58	-26	4	18.31	4.77					
	-54	-34	4	17.69	4.61					
	-46	-30	2	17.56	4.57					
	-54	-4	-14	17.55	4.57					
	-56	-10	0	17.25	4.49					
	-54	-18	10	16.11	4.19					
	-48	-24	8	15.98	4.16					
	-68	-24	10	15.93	4.15					
	-60	-2	0	15.85	4.13					
	-50	-16	4	15.43	4.02					
Middle temporal pole	-28	18	-38	8.05	2.10					
MTG						50	-24	2	18.59	4.84
						58	-34	2	18.44	4.80
						50	-16	-12	14.17	3.69

						58	-22	-4	14.04	3.66
						58	12	-18	13.91	3.62
						64	2	-16	13.55	3.53
						50	-6	-14	13.18	3.43
						44	-38	2	13.09	3.41
						54	-68	24	6.13	1.60
						62	-60	18	5.68	1.48
IFG	-22	4	-42	6.25	1.63	26	-32	-18	7.85	2.04
ITG						46	-48	-22	7.46	1.94
						40	-20	-14	6.47	1.68
Parietal										
Postcentral gyrus	-62	-8	38	6.89	1.79	62	-14	48	8.31	2.16
	-58	-12	46	6.84	1.78	56	-14	58	6.29	1.64
	-56	-14	56	5.70	1.48	26	-32	66	6.25	1.63
						50	-22	68	5.95	1.55
						70	-14	50	5.81	1.51
Angular gyrus						42	-62	26	7.04	1.83
Occipital										
SOcc						14	-96	16	6.87	1.79
						16	-90	24	6.86	1.79
MOcc						16	-88	18	6.95	1.81
						20	-94	14	6.37	1.66
						26	-90	14	5.78	1.50
Cuneous	-10	-94	18	6.48	1.69					
	-14	-90	16	6.23	1.62					
Lingual gyrus	-14	-62	-10	6.29	1.64					
Subcortical										
Hippocampus						16	-28	-6	7.74	2.02
Parahippocamal gyrus						18	-32	-10	6.58	1.71
						26	6	-30	5.79	1.51
Calcarine	-14	-82	18	5.73	1.49	14	-48	6	7.42	1.93
Mid cingulate	-6	-10	44	6.36	1.66					
	-18	-32	50	6.03	1.57					
Cerebellum										
Cerebellum lob VIIa crus II	-18	-76	-38	9.82	2.56	20	-78	-38	16.97	4.42
Cerebellum lob VIIa crus I	-58	-50	-28	7.33	1.91	16	-70	-26	14.50	3.78
Cerebellum lob VIII	-24	-62	-50	6.18	1.61	24	-70	-52	10.97	2.86
Cerebellum lob IX	-4	-54	-42	7.74	2.02	8	-52	-40	8.10	2.11
Cerebellum lob VI						32	-64	-20	7.02	1.83

Note. We show *t*-values for signal increases associated with emotion using Positive + Negative vs. Neutral, signal increases associated with neutral using Neutral vs. Positive + Negative. Coordinates are MNI space. Height threshold: $t = 6.14$, $P < .05$, FWE corrected. Extent threshold: $k = 0$ voxels.

Table 2.

Brain activity associated with true-false response, Study 1

	Left					Right				
Region label	*x*	*y*	*z*	*t*	*d*	*x*	*y*	*z*	*t*	*d*
Congruent probe										
Frontal										
Insula	-38	0	6	8.94	4.10	46	2	4	7.48	3.43
Temporal										
Superior temporal pole	-56	14	-6	9.55	4.38	60	12	-6	8.21	3.77
Fusiform gyrus	-30	-68	0	8.35	3.83	56	16	-10	7.51	3.45
	-40	-68	-20	8.68	3.98					
	-38	-46	-10	8.38	3.85					
	-36	-50	-8	7.71	3.54					
Insula	-54	-14	18	8.92	4.09					
Middle temporal gyrus	-36	-56	0	7.48	3.43					
Inferior temporal gyrus	-46	-38	-12	7.54	3.46					
Heschl's gyrus	-32	-30	2	7.48	3.43					
	-32	-24	-6	7.47	3.43					
Parietal										
Postcentral gyrus	-22	-34	74	7.91	3.63					
Angular gyrus	-46	-62	38	7.73	3.55					
Occipital										
Middle occipital	-34	-68	8	10.13	4.65					
Lingual gyrus	-14	-92	-10	8.62	3.96	8	-84	-6	9.38	4.30
	-18	-90	-12	8.58	3.94	18	-86	-10	8.99	4.12
						10	-70	-10	7.58	3.48
Inferior occipital	-28	-74	2	9.02	4.14	24	-92	-8	8.15	3.48
	-40	-70	-4	8.52	3.91	20	-92	-6	8.08	3.48
	-44	-74	-10	8.32	3.82					
Calcarine	-4	-84	-10	7.65	3.51					
Subcortical										
Putamen	-24	8	14	12.76	5.85	26	6	2	9.13	4.19
	-30	-2	0	11.59	5.32	28	2	-6	8.68	3.98
	-28	-2	6	10.9	5.00	22	2	-10	8.61	3.95
	-26	8	-2	10.83	4.97	26	-2	-8	8.25	3.79
	-28	2	-8	10.18	4.67	26	0	14	8.31	3.81
	-24	-12	8	9.88	4.53	22	-2	18	8.09	3.71
	-26	-8	-6	9.67	4.44	30	-8	4	8.26	3.79
	-28	-10	14	9.38	4.30					
	-14	2	12	9.36	4.29					
	-26	-16	12	9.15	4.20					
	-30	-4	14	8.94	4.10					
	-28	-14	4	8.83	4.05					
	-38	0	-2	8.67	3.98					
Thalamus	-20	0	-12	9.02	4.14					
Pallidium	-30	-10	-12	8.64	3.96					
Cerebellum										
Cerebellum lobule VI						28	-68	-22	10.24	4.70
						24	-70	-22	9.71	4.46
						22	-56	-20	8.4	3.85
						30	-52	-28	8.38	3.85
Cerebellum crus I						26	-66	-34	10.09	3.85
						28	-78	-26	8.84	4.06
						22	-78	-28	8.56	3.93
						24	-68	-28	7.6	3.49

						46	-58	-30	8.15	3.74
						6	-82	-18	7.99	3.67
						44	-68	-22	7.67	3.52
Cerebellum lobule VIIb						28	-72	-40	8.46	3.88
Cerebellum crus II						30	-76	-40	8.42	3.86
						12	-76	-34	7.92	3.63
Cerebellum lobule VIII						10	-62	-34	9.63	4.42
						8	-68	-46	7.49	3.44
Cerebellum lobules IV/V						28	-38	-28	7.84	3.60
						28	-42	-26	7.69	3.53
						16	-48	-16	7.6	3.49
Incongruent probe										
Frontal										
Frontal superior gyrus	-20	52	30	8.12	3.72					
	-22	52	26	8.04	3.69					
Insula						40	0	2	8.29	3.80
Temporal										
Superior temporal pole	-54	14	-4	9.28	4.26					
	-50	18	-12	8.2	3.76					
Inferior temporal gyrus	-44	-38	-10	8.52	3.91					
	-38	-46	-14	8.41	3.86					
Fusiform gyrus	-32	-74	-18	7.9	3.62	40	-60	-20	7.51	3.45
Middle temporal gyrus						68	-40	-6	7.51	3.45
Parietal										
Angular gyrus	-52	-52	32	7.74	3.55					
	-56	-52	30	7.6	3.49					
Occipital										
Middle occipital gyrus	-32	-94	-8	11.09	5.09	20	-98	4	8.01	3.68
Inferior occipital gyrus	-30	-92	-12	9.34	4.29	22	-94	-8	8.25	3.79
Lingual gyrus	-14	-34	-4	7.52	3.4	22	-86	-16	7.64	3.5
Subcortical										
Amygdala			-		4.88					4.57
	-24	2	11	10.64		20	2	-12	9.97	
	-30	-4	-14	7.49	3.44	24	-6	-10	7.53	3.46
Putamen	-24	14	-12	8.01	3.68	30	10	-6	9.11	4.18
	-26	10	-12	7.94	3.64	16	12	-4	8.53	3.91
	-22	10	14	7.53	3.46	20	10	-8	8.21	3.77
						30	6	-2	7.87	3.61
						26	-2	14	7.83	3.59
						26	4	16	7.54	3.46
						22	20	0	7.48	3.43
Caudate						18	6	16	8.17	3.75
						22	-6	22	7.85	3.60
Hippocampus	-26	-32	-4	7.8	3.58					
Cerebellum										
Cerebellum lobule VI	-20	-72	-20	8.15	3.74	34	-42	-34	7.63	3.50
	-24	-76	-20	7.89	3.62	32	-40	-36	7.6	3.49
	-20	-76	-22	7.83	3.59					
	-36	-52	-24	8.16	3.74					
	-20	-72	-20	8.15	3.74					
	-38	-66	-20	7.73	3.55					
	-38	-70	-16	7.57	3.47					
Cerebellum crus I	-22	-66	-36	7.99	3.67	28	-72	-34	7.94	3.64
						46	-68	-22	8.19	3.76
Cerebellum lobule VIII	-24	-62	-50	8.08	3.71					
	-26	-48	-52	7.61	3.49					
Cerebellum crus II						24	-78	-40	7.99	3.67

Note. We show *t*-values for signal increases associated with the true/false response in congruent trials and incongruent trials separately. Coordinates are MNI space. Height threshold: $t = 7.46$, $p < .05$, FWE corrected. Extent threshold: $k = 0$ voxels.

Appendix E: Boxplot diagrams behavioral assessments, Study 2

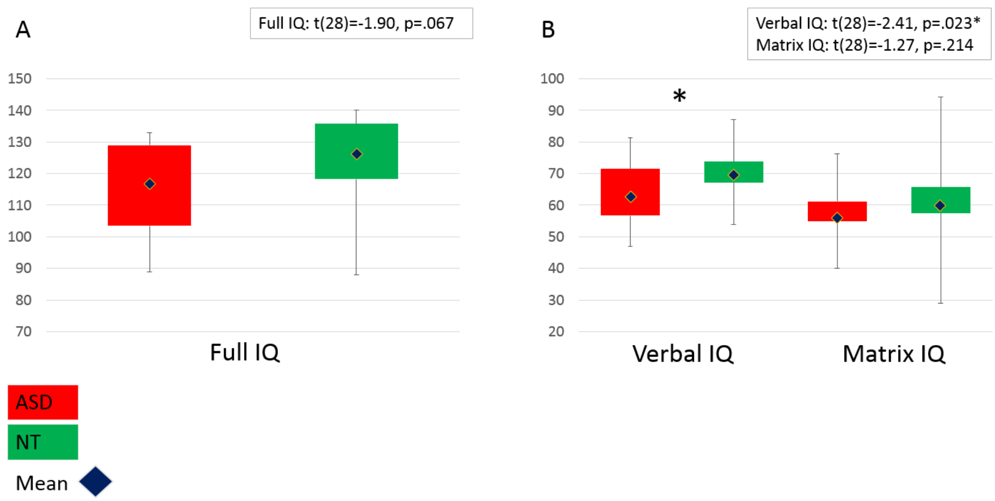


Figure 1. IQ scores from the Wechsler Abbreviated Intelligence Scales (WASI) or Wechsler Adult Intelligence Scales (WAIS); A: Full-Scale; B: Verbal-IQ and Matrix-IQ. Higher scores indicate more ability. Boxplot shows range, range between which the middle 50% of scores fall, median, upper quartile, lower quartile, and mean (blue ◊) for autism (ASD: red) and neurotypical (NT: green) groups.
* *p* < .05

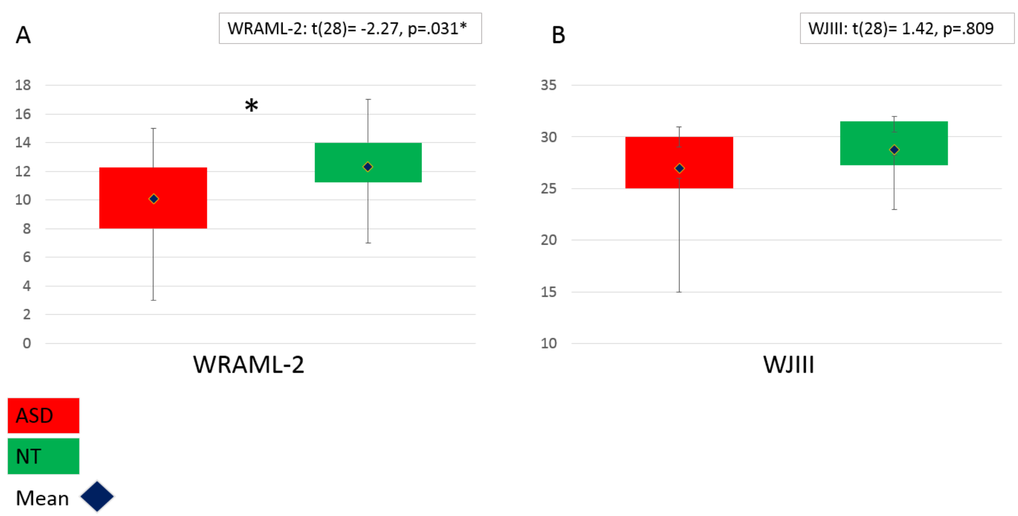


Figure 2. Language measures. A: WRAML-2 Wide Range Assessment of Memory and Learning (Rutter, Bailey & Lord, 2003) scaled (age-adjusted) scores, higher scores are consistent with better sentence repetition abilities. B: WJIII, Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock et al., 2001) scores, higher scores are consistent with better language abilities. Boxplot shows range, range between which the middle 50% of scores fall, median, upper quartile, lower quartile, and mean (blue ◊) for autism (ASD: red) and neurotypical (NT: green) groups.
* *p* < .05

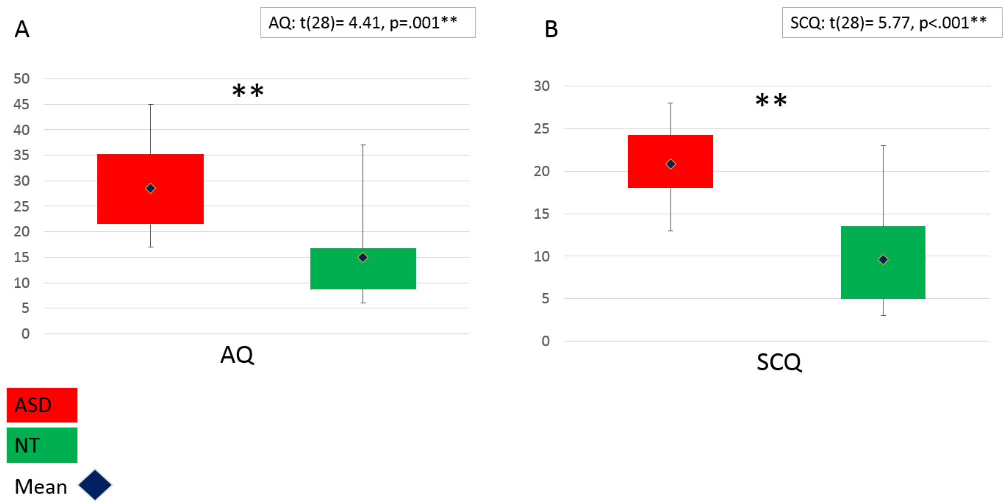


Figure 3. Autism trait measures. A: Autism Quotient (AQ) (Baron-Cohen et al., 2001) measures autistic characteristics in adults. B: Social Communication Questionnaire (SCQ) (Rutter, Bailey, & Lord, 2003) measures early development in language use and social functioning. Scores ≥ 15 suggest autistic characteristics. On both, higher scores indicate more symptoms. Boxplot shows range, range between which the middle 50% of scores fall, median, upper quartile, lower quartile, and mean (blue ◊) for autism (ASD: red) and neurotypical (NT: green) groups.
* $p < .05$, ** $p < .001$

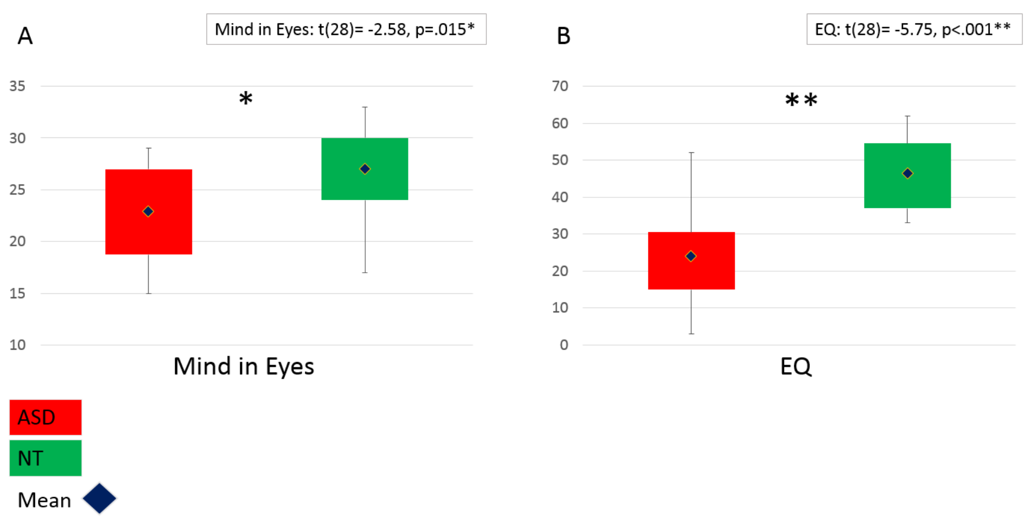


Figure 4. Empathy measures. A: Reading the Mind in the Eyes-Revised (Baron-Cohen, Wheelwright, Hill, et al., 2001) measures empathic abilities through photographs of eye regions. B: Empathy Quotient (EQ) (Baron-Cohen & Wheelwright, 2004). On both, higher scores are indicative of better empathizing abilities. Boxplot shows range, range between which the middle 50% of scores fall, median, upper quartile, lower quartile, and mean (blue ◊) for autism (ASD: red) and neurotypical (NT: green) groups.
* $p < .05$, ** $p < .001$

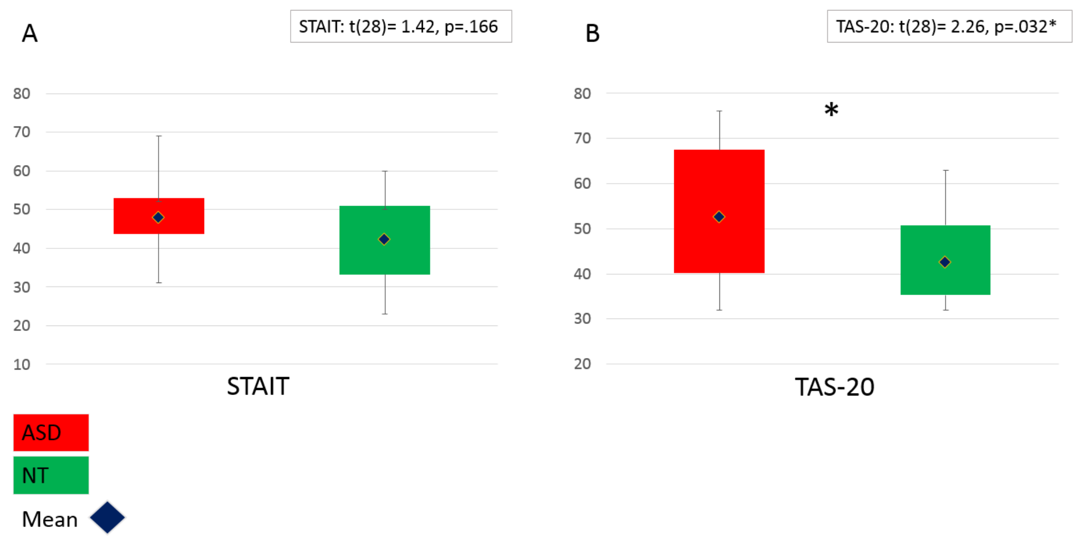


Figure 5. A: Anxiety scores derived from the STAI, State Trait Anxiety Inventory (Spielberger, 2010); higher scores suggest higher levels of anxiety. B: Alexithymia scores derived from the TAS-20, Toronto Alexithymia Scales (Bagby, Parker, et al., 1994; Bagby, Taylor, et al., 1994). Scores ≥ 61 suggest high alexithymia; scores ≤ 51 = low symptomatology. Boxplot shows range, range between which the middle 50% of scores fall, median, upper quartile, lower quartile, and mean (blue ◊) for autism (ASD: red) and neurotypical (NT: green) groups.

* $p < .05$

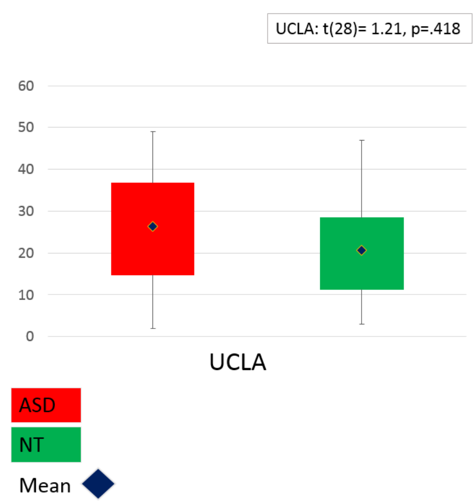


Figure 6. Loneliness scores derived from the UCLA Loneliness Questionnaire (Russell, 1996). Higher scores are indicative of higher degree of loneliness. Boxplot shows range, range between which the middle 50% of scores fall, median, upper quartile and lower quartile for autism (ASD: red) and neurotypical (NT: green) groups. Boxplot shows range, range between which the middle 50% of scores fall, median, upper quartile, lower quartile, and mean (blue ◊) for autism (ASD: red) and neurotypical (NT: green) groups.

Appendix F: Social-affective questionnaires

Table 1

Autism Quotient (AQ)

Instructions	
"Below is a list of statements. Please read each statement very carefully and rate how strongly you agree or disagree putting an "X" under your response." Response choices include "strongly agree," "slightly agree" "slightly disagree" and "slightly agree."	
Test items	
1.	I prefer to do things with others rather than on my own.
2.	I prefer to do things the same way over and over again.
3.	If I try to imagine something, I find it very easy to create a picture in my mind.
4.	I frequently get so strongly absorbed in one thing that I lose sight of other things.
5.	I often notice small sounds when others do not.
6.	I usually notice car number plates or similar strings of information.
7.	Other people frequently tell me that what I've said is impolite, even though I think it is polite.
8.	When I'm reading a story, I can easily imagine what the characters might look like.
9.	I am fascinated by dates.
10.	In a social group, I can easily keep track of several different people's conversations.
11.	I find social situations easy.
12.	I tend to notice details that others do not.
13.	I would rather go to a library than a party.
14.	I find making up stories easy.
15.	I find myself drawn more strongly to people than to things.
16.	I tend to have very strong interests which I get upset about if I can't pursue.
17.	I enjoy social chit-chat.
18.	When I talk, it isn't always easy for others to get a word in edgeways.
19.	I am fascinated by numbers.
20.	When I'm reading a story, I find it difficult to work out the characters' intentions.
21.	I don't particularly enjoy reading fiction.
22.	I find it hard to make new friends.
23.	I notice patterns in things all the time.
24.	I would rather go to the theatre than a museum.
25.	It does not upset me if my daily routine is disturbed.
26.	I frequently find that I don't know how to keep a conversation going.
27.	I find it easy to "read between the lines" when someone is talking to me.
28.	I usually concentrate more on the whole picture, rather than the small details.
29.	I am not very good at remembering phone numbers.
30.	I don't usually notice small changes in a situation, or a person's appearance.
31.	I know how to tell if someone listening to me is getting bored.

Test items	
32.	I find it easy to do more than one thing at once.
33.	When I talk on the phone, I’m not sure when it’s my turn to speak.
34.	I enjoy doing things spontaneously.
35.	I am often the last to understand the point of a joke.
36.	I find it easy to work out what someone is thinking or feeling just by looking at their face.
37.	If there is an interruption, I can switch back to what I was doing very quickly.
38.	I am good at social chit-chat.
39.	People often tell me that I keep going on and on about the same thing.
40.	When I was young, I used to enjoy playing games involving pretending with other children.
41.	I like to collect information about categories of things (e.g. types of car, types of bird, types of train, types of plant, etc.).
42.	I find it difficult to imagine what it would be like to be someone else.
43.	I like to plan any activities I participate in carefully.
44.	I enjoy social occasions.
45.	I find it difficult to work out people’s intentions.
46.	New situations make me anxious.
47.	I enjoy meeting new people.
48.	I am a good diplomat.
49.	I am not very good at remembering people’s date of birth.
50.	I find it very easy to play games with children that involve pretending.

Note. Autism Quotient (Baron-Cohen, Wheelwright, Skinner, et al., 2001).

Table 2

Social Communication Questionnaire (SCQ)

Instructions	
"Please respond to the following questions to the best of your recollection with regards to your childhood (that is, when you were about 4-5 years old)." Response choices are "yes" or "no."	
Test items	
1.	Were you able to talk using short phrases or sentences?
2.	Did you have to and fro conversations that involved taking turns or building on what is said?
3.	Did you ever use odd phrases or say the same thing over and over in almost exactly the same way (either phrases that you heard other people use or ones that you made up)?
4.	Did you ever use socially inappropriate questions or statements? For example, did you ever regularly ask personal questions or make personal comments at awkward times?
5.	Did you ever get your pronouns mixed up (e.g. saying you or she/he for I)?
6.	Did you ever use words that you invented or made up yourself; put things in odd, indirect ways; or use metaphorical ways of saying things (e.g., saying hot rain for steam)?
7.	Did you ever say the same thing over and over in exactly the same way?
8.	Did you ever have things that you had to do in a very particular way or order, or rituals that you insisted on going through?
9.	Did your facial expressions usually seem appropriate to the particular situation?
10.	Did you ever use others' hands like a tool or as if they were part of your body (e.g., pointing with someone's finger or putting someone's hand on a doorknob to get them to open the door)?
11.	Did you ever have any interests that you were preoccupied with that might seem odd to other people (e.g., traffic lights, drainpipes, or timetables)?
12.	Were you ever more interested in parts of an object, rather than in using the object as it was intended (e.g., spinning the wheels of a car)?
13.	Did you ever have any special interests that were unusual in their intensity but were otherwise appropriate for your age and peer group (e.g., trains or dinosaurs)?
14.	Were you ever unusually interested in the sight, feel, sound, taste, or smell of things or people?
15.	Did you ever have any mannerisms or odd ways of moving your hands or fingers, such as flapping or moving your fingers in front of your eyes?
16	Did you ever have any complicated movements of your whole body, such as spinning or repeatedly bouncing up and down?
17.	Did you ever injure yourself deliberately, such as biting your arm or banging your head?
18.	Did you ever have any objects that you had to carry around?

Test items	
19.	Did you have any particular friends or a best friend?
20.	Did you ever talk with others just to be friendly (rather than to get something)?
21.	Did you ever spontaneously copy other people or what they were doing (such as vacuuming, gardening, or mending things)?
22.	Did you ever spontaneously point at things just to show others (not because you want them)?
23.	Did you ever use gestures, other than pointing or pulling someone's hand, to let others know what you wanted?
24.	Did you nod your head to indicate yes?
25.	Did you shake your head to indicate no?
26.	Did you usually look people directly in the face when doing things with them or talking with them?
27.	Did you smile back if someone smiled at you?
28.	Did you ever show people things that interested you to engage their attention?
29.	Did you ever offer to share things other than food?
30.	Did you ever want others to join in your enjoyment of something?
31.	Did you ever try to comfort others if they were sad or hurt?
32.	If you wanted something or wanted help, did you look at others and use gestures with sounds or words to get their attention?
33.	Did you show a normal range of facial expressions?
34.	Did you ever spontaneously join in and try to copy the actions of others in social games (such as “The Mulberry Bush” or “London Bridge is Falling Down”)?
35.	Did you play any pretend or make-believe games?
36.	Were you interested in other children of approximately the same age who you did not know?
37.	Did you respond positively when another child approached you?
38.	If someone came into a room and started talking to you without calling your name, did you usually look up and pay attention?
39.	Did you ever play imaginative games with another child in such a way that each child understood what the other was pretending?
40.	Did you play cooperatively in games that needed some form of joining in with a group of other children (such as hide-and-seek or ball games)?

Note. Social Communication Questionnaire (Rutter et al., 2003).

Table 3

Empathy Quotient (EQ)

Instructions	
"Below is a list of statements. Please read each statement very carefully and rate how strongly you agree or disagree putting an "X" under your response." Response choices include "strongly agree," "slightly agree" "slightly disagree" and "slightly agree."	
Test items	
1.	I can easily tell if someone else wants to enter a conversation.
2.	I prefer animals to humans.
3.	I try to keep up with the current trends and fashions.
4.	I find it difficult to explain to others things that I understand easily, when they don't understand it first time.
5.	I dream most nights.
6.	I really enjoy caring for other people.
7.	I try to solve my own problems rather than discussing them with others.
8.	I find it hard to know what to do in a social situation.
9.	I am at my best first thing in the morning.
10.	People often tell me that I went too far in driving my point home in a discussion.
11.	It doesn't bother me too much if I am late meeting a friend.
12.	Friendships and relationships are just too difficult, so I tend not to bother with them.
13.	I would never break a law, no matter how minor.
14.	I often find it difficult to judge if something is rude or polite.
15.	In a conversation, I tend to focus on my own thoughts rather than on what my listener might be thinking.
16.	I prefer practical jokes to verbal humor.
17.	I live life for today rather than the future.
18.	When I was a child, I enjoyed cutting up worms to see what would happen.
19.	I can pick up quickly if someone says one thing but means another.
20.	I tend to have very strong opinions about morality.
21.	It is hard for me to see why some things upset people so much.
22.	I find it easy to put myself in somebody else's shoes.
23.	I think that good manners are the most important thing a parent can teach their child.
24.	I like to do things on the spur of the moment.
25.	I am good at predicting how someone will feel.
26.	I am quick to spot when someone in a group is feeling awkward or uncomfortable.
27.	If I say something that someone else is offended by, I think that that's their problem, not mine.
28.	If anyone asked me if I liked their haircut, I would reply truthfully, even if I didn't like it.
29.	I can't always see why someone should have felt offended by a remark.

Test items	
30.	People often tell me that I am very unpredictable.
31.	I enjoy being the center of attention at any social gathering.
32.	Seeing people cry doesn’t really upset me.
33.	I enjoy having discussions about politics.
34.	I am very blunt, which some people take to be rudeness, even though this is unintentional.
35.	I don’t tend to find social situations confusing.
36.	Other people tell me I am good at understanding how they are feeling and what they are thinking.
37.	When I talk to people, I tend to talk about their experiences rather than my own.
38.	It upsets me to see an animal in pain.
39.	I am able to make decisions without being influenced by people’s feelings.
40.	I can’t relax until I have done everything I had planned to do that day.
41.	I can easily tell if someone else is interested or bored with what I am saying.
42.	I get upset if I see people suffering on news programs.
43.	Friends usually talk to me about their problems as they say that I am very understanding.
44.	I can sense if I am intruding, even if the other person doesn’t tell me.
45.	I often start new hobbies but quickly become bored with them and move on to something else.
46.	People sometimes tell me that I have gone too far with teasing.
47.	I would be too nervous to go on a big rollercoaster.
48.	Other people often say that I am insensitive, though I don’t always see why.
49.	If I see a stranger in a group, I think that it is up to them to make an effort to join in.
50.	I usually stay emotionally detached when watching a film.
51.	I like to be very organized in day-to-day life and often make lists of the chores I have to do.
52.	I can tune into how someone else feels rapidly and intuitively.
53.	I don’t like to take risks.
54.	I can easily work out what another person might want to talk about.
55.	I can tell if someone is masking their true emotion.
56.	Before making a decision I always weigh up the pros and cons.
57.	I don’t consciously work out the rules of social situations.
58.	I am good at predicting what someone will do.
59.	I tend to get emotionally involved with a friend’s problems.
60.	I can usually appreciate the other person’s viewpoint, even if I don’t agree with it.

Note. Two types of questions are included on the EQ (Simon Baron-Cohen & Wheelwright, 2004), 40 empathy-related and 20 fillers (highlighted in grey).

Table 4

Toronto Alexithymia Scale (TAS-20)

Instructions	
"Using the scale provided as a guide, indicate how much you agree or disagree with each of the following statements by circling the corresponding number. Response choices include: "strongly disagree," "moderately disagree," "neither disagree nor agree," "moderately agree," and "strongly agree."	
Test items	
1.	I am often confused about what emotion I am feeling.
2.	It is difficult for me to find the rights words for my feelings
3.	I have physical sensations that even doctors don't understand.
4.	I am able to describe my feelings easily.
5.	I prefer to analyze problems rather than just describe them.
6.	When I am upset, I don't know if I am sad, frightened, or angry.
7.	I am often puzzled by sensations in my body.
8.	I prefer to just let things happen rather than to understand why they turned out that way.
9.	I have feelings that I can't quite identity.
10.	Being in touch with emotions is essential.
11.	I find it hard to describe how I feel about people.
12.	People tell me to describe my feelings more.
13.	I don't know what's going on inside me.
14.	I often don't know why I am angry.
15.	I prefer talking to people about their daily activities rather than their feelings.
16	I prefer to watch "light" entertainment shows rather than psychological dramas.
17.	It is difficult for me to reveal my innermost feelings, even to my close friends.
18.	I can feel close to someone, even in moments of silence.
19.	I find examination of my feelings useful in solving personal problems.
20.	Looking for hidden meanings in movies or play distracts from their enjoyment.

Note. Toronto Alexithymia Scales – 20 Items (Parker et al., 2003)

Table 5.

Reading the mind in the Eyes (MinE)

Instructions

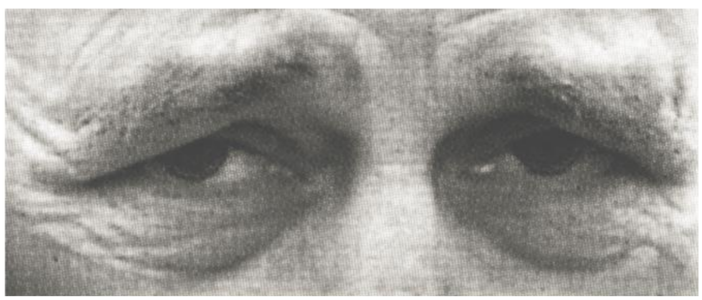
"For each set of eyes, choose and circle which word best describes what the person in the picture is thinking or feeling. You may feel that more than one word is applicable but please choose just one word, the word you consider to be most suitable. Before making your choice, make sure that you have read all 4 words. You should try to do the task as quickly as possible but you will not be timed. If you really don't know what a word means you can look it up in the definition handout."

Test items

playful | 1 | comforting

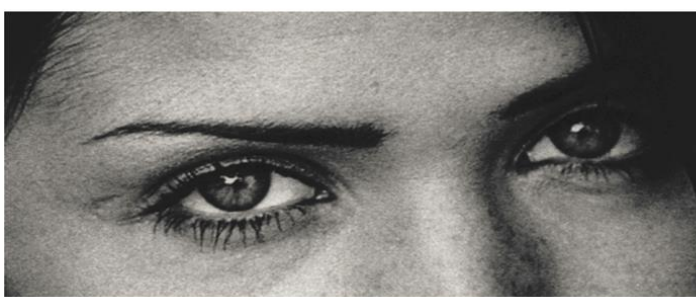
irritated | bored

terrified | 2 | upset



arrogant | annoyed

joking | 3 | flustered



desire | convinced

	4	
joking		insisting
amused		relaxed
	5	
irritated		sarcastic
worried		friendly
	6	
aghast		fantasizing
impatient		alarmed
	7	
apologetic		friendly
uneasy		dispirited

8

despondent relieved

shy excited

9

annoyed hostile

horrified preoccupied

10

cautious insisting

bored aghast

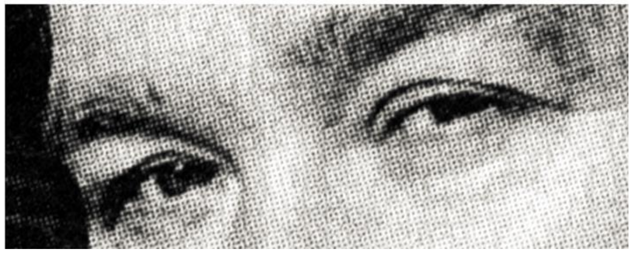
11

terrified amused

regretful flirtatious

12

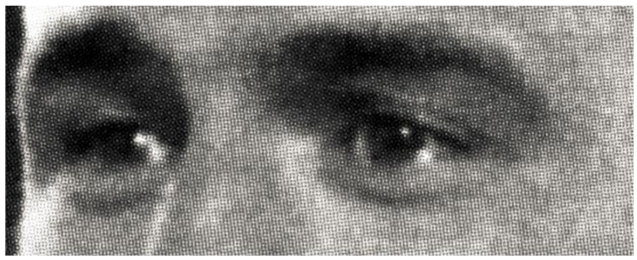
indifferent | embarrassed



skeptical | dispirited

13

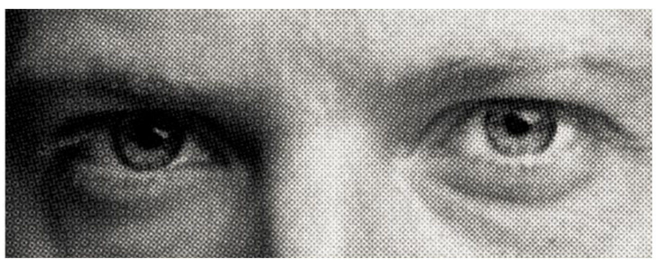
decisive | anticipating



threatening | shy

14

irritated | disappointed



depressed | accusing

15

contemplative | flustered

encouraging | amused

16

irritated

thoughtful

encouraging

sympathetic

17

doubtful

affectionate

playful

aghast

18

decisive

amused

aghast

bored

19

arrogant

grateful

sarcastic

tentative

20

dominant | friendly

guilty | horrified

21

embarrassed | fantasizing

confused | panicked

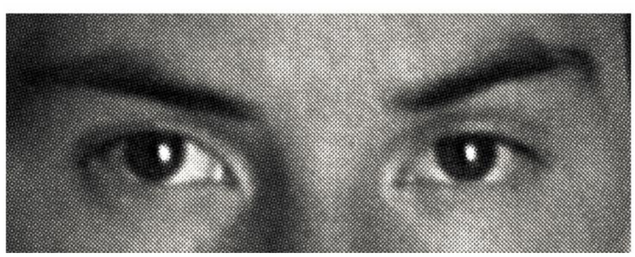
22

preoccupied | grateful

insisting | imploring

23

contented | apologetic



defiant | curious

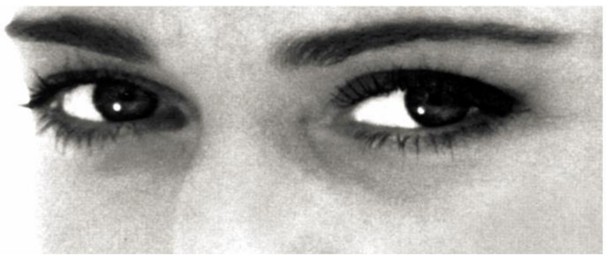
24

pensive irritated

excited hostile

25

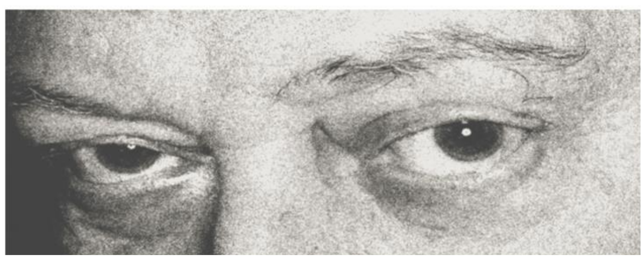
panicked incredulous



despondent interested

26

alarmed shy



hostile anxious

27

joking cautious

arrogant reassuring

28

interested | joking

affectionate | contented

29

impatient | aghast

irritated | reflective

30

grateful | flirtatious

hostile | disappointed

31

ashamed | confident

joking | dispirited

32

serious ashamed

bewildered alarmed

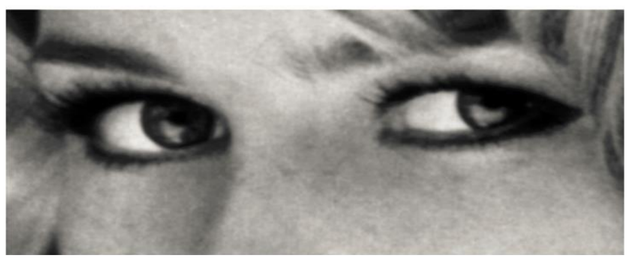
33

embarrassed guilty

fantasizing concerned

34

aghast baffled



distrustful terrified

35

puzzled nervous

insisting contemplative

36

ashamed nervous

suspicious indecisive

Note. Reading the Mind in the Eyes (Baron-Cohen, Wheelwright, Hill, et al., 2001). A glossary of definitions is provided to participants for reference if needed. Correct responses are highlighted in green.

Table 6

State Trait Anxiety Inventory-Trait (STAIT)

Instructions

"A number of statements which people have used to describe themselves are given below. Read each statement and then, from the choices listed below, choose the best response based on how you GENERALLY feel. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe how you generally feel."

Test items

1.	I feel pleasant.
2.	I feel nervous and restless.
3.	I feel satisfied with myself.
4.	I wish I could be as happy as others seem to be.
5.	I feel like a failure.
6.	I feel rested.
7.	I am calm, cool, and collected.
8.	I feel that difficulties are piling up so that I cannot overcome them.
9.	I worry too much over something that really doesn't matter.
10.	I am happy.
11.	I have disturbing thoughts.
12.	I lack self-confidence.
13.	I feel secure.
14.	I make decisions easily.
15.	I feel inadequate.
16	I am content.
17.	Some unimportant thoughts run through my mind and bother me.
18.	I take disappointments so keenly that I can't put them out of my mind.
19.	I am a steady person.
20.	I get in a state of tension or turmoil as I think over my recent concerns and interests.

Note. State Trait Anxiety Inventory – Trait (Sesti, 2000).

Table 7

UCLA Loneliness Questionnaire (UCLA)

Instructions	
"Indicate how often each of the statements below is descriptive of you." Response choices: "I often feel this way," "I sometimes feel this way," I rarely feel this way," and "I never feel this way."	
Test items	
1	I am unhappy doing so many things alone.
2.	I have nobody to talk to.
3.	I cannot tolerate being so alone.
4.	I lack companionship.
5.	I feel as if nobody really understands me.
6.	I find myself waiting for people to call or write.
7.	There is no one I can turn to.
8.	I am no longer close to anyone.
9.	My interests and ideas are not shared by those around me.
10.	I feel left out.
11.	I feel completely alone.
12.	I am unable to reach out and communicate with those around me.
13.	My social relationships are superficial.
14.	I feel starved for company.
15.	No one really knows me well.
16.	I feel isolated from others.
17.	I am unhappy being so withdrawn.
18.	It is difficult for me to make friends.
19.	I feel shut out and excluded by others.
20.	People are around me but not with me.

Note. UCLA Loneliness questionnaire (Russell, 1996).

Appendix G: Behavioral results, Study 2

Table 1.

Accuracy and response time results, Study 2

	ASD Mean (SD)	NT Mean (SD)	*t*(28)	Cohen's *d*
Accuracy (*% correct*)				
PosCon	96.43 (9.64)	97.74 (6.67)	-0.44	-0.16
PosIncon	98.20 (3.58)	95.50 (10.16)	1.00	0.37
NegCon	94.64 (10.64	94.76 (11.81)	-0.03	-0.01
NegIncon	87.89 (21.02)	95.28 (10.61)	-1.24	-0.45
NeutCon	96.41 (5.41)	96.16 (4.54)	0.14	-0.05
NeutIncon	86.30 (19.49)	93.23 (9.67)	-1.21	-0.44
Response time (sec)				
PosCon	1.23 (.31)	1.13 (.41)	1.21	0.44
PosIncon	1.34 (.41)	1.13 (.24)	1.75	0.64
NegCon	1.40 (.26)	1.22 (.22)	2.01	0.74
NegIncon	1.57 (.52)	1.23 (.24)	2.34	0.86
NeutCon	1.42 (.43)	1.23 (.32)	1.42	0.52
NeutIncon	1.66 (.43)	1.45 (.34)	1.53	0.56

Note. Means (standard deviations) of EIT accuracy and response time (correct items only; 5.46% of data removed). 72 items were distributed evenly over the 3 conditions (36 each POS, NEG, NEUT) and congruency (18 each CON, INCON). ASD (n = 14), NT) (n = 16).

Appendix H: Whole-brain neural results, Study 2

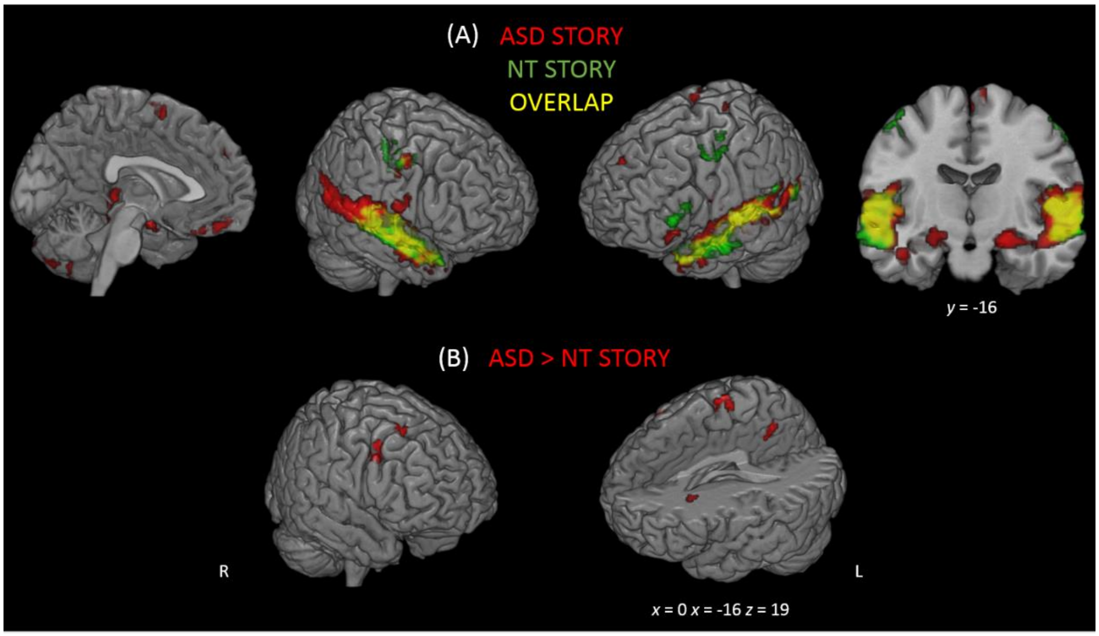


Figure 1. Within- and between-group scenario-related activity, Study 2. (A) Contrast of all scenarios (POS+NEG+NEUT) in autism (ASD; red), neurotypical control group (NT; green), and overlap yellow. (B) Regions showing differential activation between groups related to all story conditions; ASD > NT (red), NT > ASD (green). Task-related activity is displayed using a cluster corrected threshold of $p < .001$.

Table 1

Within- and between group scenario-related brain activations, Study 2

Region label	**Lat**	**Vol**	***x***	***y***	***z***	***t***	***Z***
ASD							
Frontal							
IFG (triangularis)	L	203	-44	20	24	5.59	4.54
[a]	L	[a]	-52	22	18	4.71	4.01
IFG (opercularis)	L	[a]	-52	12	20	4.61	3.94
IFG (triangularis)	L	203	-44	20	24	5.59	4.54
SMA	-	96	0	4	66	5.50	4.49
IFG (orbitalis)	L	157	-50	26	-6	5.24	4.34
Precentral gyrus	R	101	52	-2	48	5.15	4.29
Postcentral gyrus	R	[a]	56	-8	38	3.76	3.36
	L	87	-30	-28	66	5.10	4.25
Paracentral lob	L	[a]	-8	-34	74	4.16	3.64
Postcentral gyrus	L	[a]	-18	-28	74	4.15	3.63
SMA	R	81	6	-16	72	5.02	4.20
Precentral gyrus	R	[a]	12	-22	78	3.72	3.33
vmPFC (rectus)	-	161	0	46	-20	4.66	3.98
[a]	-	[a]	2	28	-26	4.45	3.84
[a]	L	[a]	-6	34	-20	3.58	3.22
dmPFC	L	107	-8	50	34	4.54	3.90
[a]	L	[a]	-10	42	46	4.10	3.60
[a]	L	[a]	-10	42	46	4.10	3.60
Postcentral gyrus	L	81	-52	-6	46	4.29	3.73
Temporal							
STS	R	7062	48	-16	6	11.11	6.82
[a]	R	[a]	58	-14	0	9.74	6.39
Lingual gyrus	R	[a]	12	-28	-6	9.38	6.26
pSTS	R	[a]	66	-28	10	9.34	6.24
STS	R	[a]	56	-22	8	8.69	6.00
Heschl's gyrus	L	6452	-44	-22	12	10.97	6.78
STS	L	[a]	-56	-22	10	10.57	6.66
MTG	L	[a]	-62	-16	-2	8.03	5.74
[a]	L	[a]	-66	-38	10	7.95	5.70
STS	L	[a]	-48	-16	2	7.39	5.46
Cerebellum							
Cerebellum lob VI	L	648	-14	-68	-24	6.71	5.14
Cerebellum Crus 2	L	[a]	-16	-74	-38	6.55	5.06
Cerebellum lob VI	L	[a]	-20	-56	-22	5.02	4.21
Cerebellum Crus 2	L	[a]	-12	-82	-32	5.00	4.19
[a]	L	[a]	-26	-82	-38	4.63	3.96
	R	558	22	-80	-40	6.42	4.99
Cerebellum lob VI	R	[a]	18	-68	-30	5.64	4.57
Cerebellum lob VIII	R	[a]	22	-68	-40	4.98	4.18
Cerebellum lob VIII	L	143	-24	-58	-52	6.29	4.93
[a]	L	[a]	-14	-62	-50	4.46	3.84
NT							
Frontal							
Precentral gyrus	L	183	-48	-4	54	6.17	4.86
[a]	L	[a]	-46	-12	60	4.17	3.65
Postcentral gyrus	R	129	58	-14	50	5.59	4.54

Region label	**Lat**	**Vol**	***x***	***y***	***z***	***t***	***Z***
Precentral gyrus	R	[a]	52	-20	58	4.90	4.13
[a]	R	[a]	52	6	48	4.27	3.72
[a]	R	[a]	56	-4	46	4.09	3.59
IFG (triangularis)	L	256	-58	32	8	5.57	4.53
[a]	L	[a]	-58	22	18	4.51	3.88
[a]	L	[a]	-52	22	0	4.44	3.83
Temporal							
STS	L	4541	-54	-22	0	9.75	6.39
[a]	L	[a]	-62	-20	6	9.39	6.26
[a]	L	[a]	-42	-22	6	8.72	6.01
[a]	L	[a]	-62	-32	6	8.63	5.98
[a]	L	[a]	-52	-8	-6	7.56	5.54
MTG	R	3554	62	-18	0	8.64	5.98
Heschl's gyrus	R	[a]	48	-16	6	8.64	5.98
MTG	R	[a]	62	2	-16	8.28	5.84
aSTS	R	[a]	48	18	-20	7.59	5.55
MTG	R	[a]	64	-12	-10	7.55	5.53
Cerebellum							
Cerebellum crus 2	R	232	20	-80	-40	6.47	5.02
Cerebellum lob VI	R	[a]	20	-70	-28	4.92	4.14
Cerebellum crus 2	L	103	-20	-76	-38	5.54	4.51
ASD > NT							
Frontal							
IFG	L	133	-28	26	28	5.63	4.57
[a]	L	[a]	-26	16	22	4.79	4.06
Precuneus	R	123	8	-52	36	5.58	4.54
[a]	-	[a]	4	-56	46	3.81	3.39
SMA	R	122	8	-18	72	5.19	4.31
[a]	R	[a]	14	-12	60	4.41	3.81
Paracentral lob	-	[a]	-4	-28	68	3.67	3.29
IFG (opercularis)	R	105	52	16	34	4.99	4.19
m frontal	R	101	24	18	46	4.78	4.05
[a]	R	[a]	30	22	56	4.34	3.76
Cerebellum							
Cerebellum crus 2	L	137	-36	-72	-44	4.66	3.98
Cerebellum crus 1	L	[a]	-36	-64	-30	4.6	3.94
Cerebellum crus 2	L	[a]	-28	-82	-40	3.5	3.16

Note. We show *t*-values for signal increases for the average effect of all stories (POS+NEG+NEUT) in autism (ASD), neurotypical (NT), ASD > NT. NT > ASD results not significant. Laterality (Lat), right (R), left (L) and medial ('-'). Number of voxels in each cluster (Voxel), XYZ coordinates, *t*-values and *z*-scores. Coordinates are MNI space. Height threshold $t = 3.41$ $p < .001$ cluster corrected.
[a] Subpeaks of larger cluster immediately above.

Table 2.

Within- and between group emotion-related brain activations, Study 2

Region label	**Lat**	***voxels***	***x***	***y***	***z***	***t***	***Z***
ASD							
Frontal							
vmPFC	-	361	0	52	-12	6.28	4.92
vmPFC (rectus)	R	[a]	6	24	-22	4.67	3.98
[a]	-	[a]	0	32	-20	3.90	3.46
dmPFC	L	282	-10	50	28	5.36	4.41
[a]	L	[a]	-12	40	42	5.05	4.22
mPFC	L	[a]	-8	60	18	3.65	3.27
Precentral gyrus	R	101	54	-2	48	5.09	4.24
Postcentral gyrus	R	[a]	58	-8	38	4.71	4.01
IFG (triangularis)	L	204	-46	22	20	5.07	4.24
[a]	L	[a]	-54	26	12	4.35	3.77
Subcortical							
Hippocampus	R	668	20	-6	-16	8.40	5.89
Thalamus	L	[a]	-12	-28	0	6.88	5.22
Lingual gyrus	R	[a]	14	-26	-8	6.64	5.11
Parahippocampus	R	[a]	20	-16	-18	6.30	4.93
Vermis	R	[a]	4	-36	-6	4.74	4.03
Hippocampus	L	201	-22	-8	-14	6.52	5.04
[a]	L	[a]	-30	-18	-14	5.39	4.42
Parahippocampus	L	[a]	-12	-4	-20	3.86	3.43
Amygdala	L	[a]	-30	-2	-22	3.84	3.41
Temporal							
Heschl’s gyrus	R	5789	50	-14	6	9.89	6.44
[a]	R	[a]	42	-22	10	7.83	5.65
pSTS	R	[a]	54	-26	10	7.79	5.63
[a]	R	[a]	66	-22	8	7.68	5.59
[a]	R	[a]	62	2	-10	7.22	5.38
STS	L	5825	-44	-26	12	9.29	6.23
[a]	L	[a]	-48	-14	0	8.20	5.81
MTG	L	[a]	-62	-14	-4	7.50	5.51
[a]	L	[a]	-62	-42	4	7.36	5.44
[a]	L	[a]	-70	-28	6	7.35	5.44
Parietal							
Precuneus	R	228	8	-54	38	5.48	4.48
pCC	-	[a]	0	-52	30	5.27	4.36
Precuneus	L	[a]	-12	-54	34	4.22	3.68
[a]		[a]	16	-50	32	4.00	3.52
Cerebellum							
Cerebellum lob VI	R	245	16	-68	-24	5.88	4.70
Cerebellum Crus 2	R	[a]	26	-82	-34	4.71	4.01
[a]	R	[a]	16	-74	-38	4.01	3.54
Cerebellum lob VIII	L	329	-18	-70	-38	5.48	4.48
Cerebellum Crus 2	L	[a]	-14	-80	-34	4.99	4.18
Cerebellum Crus 1	L	[a]	-16	-70	-26	4.82	4.08
Cerebellum lob XIIb	L	[a]	-16	-78	-44	4.05	3.56
NT							
Frontal							
IFG (triangularis)	L	150	-54	24	10	5.43	4.45

Region label	Lat	*voxels*	*x*	*y*	*z*	*t*	*Z*
[a]	L	[a]	-52	22	0	3.65	3.27
dmPFC (rectus)	-	154	-2	36	-24	5.21	4.32
[a]	-	[a]	-4	46	-20	4.54	3.90
Temporal							
STS	R	3621	62	-16	-2	9.02	6.13
MTG	R	[a]	62	2	-16	8.90	6.08
Heschl's gyrus	R	[a]	48	-16	6	8.67	6.00
aSTS	R	[a]	54	8	-20	7.54	5.53
STS	L	4792	-54	-22	0	8.72	6.01
[a]	L	[a]	-62	-20	6	8.53	5.94
MTG	L	[a]	-62	-32	6	8.49	5.93
[a]	L	[a]	-58	-16	-12	8.20	5.81
Heschl's gyrus	L	[a]	-36	-28	14	7.90	5.68
ASD > NT							
Parietal							
Precuneus	R	143	8	-54	38	5.33	4.39

Note. We show *t*-values for signal increases for the average effect of emotional stories (EMO) in autism (ASD), neurotypical (NT) control group, and ASD > NT. No clusters survive in NT > ASD comparison. Laterality (Lat), right (R), left (L) or medial ('-'), number of voxels in each cluster (Voxel), XYZ coordinates, *t*-values and *z*-scores. Coordinates are MNI space. Height threshold $t = 3.24$, $p < .001$ cluster corrected.

[a] Subpeaks of larger cluster immediately above.

Table 3.

Within- and between-group valence-related brain activations, Study 2

Region label	Lat	*voxels*	*x*	*y*	*z*	*t*	*Z*
NEGATIVE							
ASD							
Frontal							
vmPFC (rectus)	-	289	2	48	-20	5.93	4.73
[a]	L	[a]	-8	46	-18	4.87	4.11
[a]	-	[a]	2	32	-18	3.91	3.46
dmPFC	R	430	10	48	24	5.79	4.66
[a]	L	[a]	-8	48	24	5.22	4.33
[a]	L	[a]	-8	48	40	5.03	4.21
IFG (orbitalis)	L	117	-52	28	-4	5.38	4.42
[a]	L	[a]	-40	32	-10	3.72	3.32
Postcentral gyrus	R	132	58	-8	38	5.09	4.25
Precentral gyrus	R	[a]	54	-2	48	4.81	4.07
IFG (triangularis)	L	239	-44	20	22	4.91	4.14
[a]	L	[a]	-54	26	12	4.73	4.02
Temporal							
Heschl’s gyrus	R	5909	50	-14	6	12.24	7.14
[a]	R	[a]	42	-22	10	9.64	6.35
STG	R	[a]	66	-26	10	8.86	6.07
[a]	R	[a]	54	-26	10	8.77	6.03
[a]	R	[a]	62	2	-10	8.30	5.85
	L	6173	-50	-24	6	11.21	6.85
[a]	L	[a]	-48	-14	0	9.78	6.40
MTG	L	[a]	-62	-14	-4	8.78	6.04
[a]	L	[a]	-62	-40	6	8.17	5.79
[a]	L	[a]	-70	-28	6	8.10	5.77
Parietal							
Precuneus	R	111	6	-56	36	5.16	4.29
[a]	R	[a]	16	-52	36	3.58	3.22
Limbic							
Hippocampus	R	503	22	-6	-16	10.50	6.63
[a]	R	[a]	16	-22	-14	7.01	5.29
[a]	R	[a]	14	-24	-4	6.76	5.17
Amygdala	R	[a]	32	0	-16	4.56	3.91
[a]	R	[a]	6	-32	-8	4.15	3.63
	L	245	-22	-8	-14	7.02	5.29
[a]	L	[a]	-30	-4	-20	5.09	4.24
Hippocampus	L	[a]	-30	-18	-14	5.68	4.59
[a]	L	[a]	-34	-28	-12	4.05	3.56
Sub lobar							
Thalamus	L	114	-12	-28	2	6.52	5.04
vmPFC (rectus)	L	[a]	-8	-28	-8	4.49	3.86
Cerebellum							
Cerebellum VI	R	361	16	-66	-26	6.55	5.06
Cerebellum crus 2	R	[a]	24	-78	-40	5.58	4.54
Cerebellum crus 1	R	[a]	28	-66	-40	4.10	3.60
[a]	R	[a]	22	-80	-26	3.61	3.42
Cerebellum IX	L	136	-8	-54	-42	5.85	4.69
[a]	-	[a]	4	-50	-42	5.09	4.25
Cerebellum XIII	L	310	-16	-68	-38	5.84	4.69

Region label	**Lat**	***voxels***	***x***	***y***	***z***	***t***	***Z***
Cerebellum XIIb	L	[a]	-16	-78	-44	4.83	4.09
Cerebellum VI	L	[a]	-16	-72	-26	4.40	3.81
Cerebellum crus 2	L	[a]	-24	-78	-30	3.76	3.35
NT							
Frontal							
IFG (triangularis)	L	126	-54	24	10	5.04	4.22
Temporal							
STG	R	3311	62	-16	-2	9.52	6.31
[a]	R	[a]	58	-2	-2	6.95	5.26
[a]	R	[a]	54	-30	6	6.75	5.16
Heschl's gyrus	R	[a]	48	-16	6	8.87	6.07
MTG	R	[a]	62	2	-16	7.47	5.50
	L	4237	-54	-22	0	9.20	6.19
[a]	L	[a]	-62	-32	6	8.68	6.00
[a]	L	[a]	-60	-8	-12	7.74	5.61
STS	L	[a]	-62	-20	6	9.14	6.17
[a]	L	[a]	-36	-34	12	8.09	5.76
Parietal							
Postcentral gyrus	R	99	54	-14	54	5.79	4.66
[a]	R	[a]	60	-6	42	4.58	3.93
Precentral gyrus	R	[a]	54	2	46	3.70	3.31
Cerebellum							
Cerebellum crus II	R	127	18	-78	-38	5.01	4.20
Cerebellum VI	R	[a]	18	-70	-26	4.32	3.75
Cerebellum crus II	L	107	-22	-76	-36	5.00	4.19
ASD > NT							
Parietal							
Precuneus	R	113	6	-56	36	5.17	4.29
[a]	R	[a]	16	-52	38	4.43	3.83
POSITIVE							
ASD							
Frontal							
Precentral gyrus	R	146	56	-2	48	5.85	4.69
Postcentral gyrus	R	[a]	56	-8	38	4.37	3.78
vmPFC (orbitalis)	-	466	0	54	-12	5.71	4.61
[a]	L	[a]	-6	46	-14	5.51	4.5
vmPFC (rectus)	R	[a]	6	44	-16	5.49	4.48
[a]	-	[a]	0	34	-22	4.42	3.82
[a]	R	[a]	6	22	-22	4.27	3.72
dmPFC	L	242	-8	50	28	5.52	4.50
[a]	L	[a]	-12	48	42	5.19	4.31
[a]	L	[a]	-10	58	16	3.79	3.38
IFG (triangularis)	L	168	-46	22	20	4.98	4.18
Temporal							
Heschl's gyrus	R	6382	50	-14	6	14.17	7.61
[a]	R	[a]	40	-24	10	10.30	6.57
STG	R	[a]	58	-16	0	9.55	6.32
[a]	R	[a]	54	-26	10	9.40	6.27
[a]	R	[a]	66	-28	10	9.21	6.20
	L	6416	-50	-24	6	11.88	7.04
[a]	L	[a]	-48	-14	0	9.90	6.44
[a]	L	[a]	-62	-14	-4	8.80	6.06
Heschl's gyrus	L	[a]	-36	-26	12	10.72	6.70

Region label	Lat	*voxels*	*x*	*y*	*z*	*t*	*Z*
MTG	L	*a*	-62	-42	4	8.30	5.85
Limbic							
Hippocampus	R	582	16	-26	-8	8.21	5.81
a	L	*a*	-16	-26	-6	7.22	5.38
a	R	*a*	20	-6	-16	6.98	5.27
Lingual gyrus	R	*a*	10	-30	0	6.01	4.77
Parahippocampus	R	*a*	20	-16	-18	5.57	4.53
Hippocampus	L	186	-22	-12	-16	6.39	4.98
a	L	*a*	-30	-18	-14	3.96	3.50
pCC	-	357	-4	-50	26	5.44	4.46
Precuneus (parietal)	R	*a*	8	-54	38	5.04	4.22
a	R	*a*	16	-50	30	4.70	4.00
a	L	*a*	-16	-54	34	4.55	3.91
Cerebellum							
Cerebellum VIII	L	335	-18	-72	-38	5.65	4.58
Cerebellum VI	L	*a*	-16	-72	-26	5.02	4.20
Cerebellum crus II	L	*a*	-12	-84	-32	4.71	4.01
a	L	*a*	-26	-82	-36	3.89	3.45
NT							
Frontal							
vmPFC (rectus)	-	368	-2	34	-24	6.18	4.87
a	L	*a*	-6	48	-18	5.61	4.56
a	-	*a*	-2	16	-28	5.41	4.44
a	-	*a*	4	42	-22	5.08	4.24
vmPFC (orbitalis)	-	*a*	0	54	-12	4.63	3.96
IFG (triangularis)	L	161	-54	24	10	5.57	4.53
a	L	*a*	-52	22	0	3.97	3.51
dmPFC	L	95	-10	52	34	5.03	4.21
Temporal							
Heschl’s gyrus	R	3769	48	-16	6	11.34	6.89
STG	R	*a*	62	-16	-2	9.81	6.41
a	R	*a*	58	-2	-2	7.30	5.42
MTG	R	*a*	62	2	-16	9.75	6.39
aSTS	R	*a*	50	18	-20	7.27	5.41
STG	L	5091	-50	-24	4	10.35	6.59
a	L	*a*	-62	-20	6	9.64	6.35
a	L	*a*	-36	-26	12	9.55	6.32
a	L	*a*	-58	-16	-12	9.34	6.24
MTG	L	*a*	-62	-32	8	9.16	6.18
Limbic							
Hippocampus	R	93	22	-16	-16	5.65	4.58
Parahippocampus	R	*a*	14	-4	-22	4.19	3.66
ASD > TD							
Frontal							
SFG	R	110	24	20	44	4.73	4.02
MFG	R	*a*	28	14	52	3.96	3.50
Parietal							
Precuneus	L	103	16	-52	38	5.56	4.53
Cerebellum							
Cerebellum crus II	L	118	-8	-84	-30	4.97	4.18

Note. We show *t*-values for signal increases for the average effect of negative (NEG) and positive (POS) for ASD (autism), NT (neurotypical) control groups, and ASD > NT. NT > ASD contrasts failed to yield significant results. Laterality (Lat) right (R) or left (L), number of voxels in each

cluster (Voxel), XYZ coordinates, *t*-values and *z*-scores. Coordinates are MNI space. Height threshold POS $t = 3.18$; NEG $t = 3.41$, $p < .001$ cluster corrected.

[a] Subpeaks of larger cluster immediately above.

Table 4.

Within group neutral-related brain activations, Study 2

Region label	Lat	*voxels*	*x*	*y*	*z*	*t*	*Z*
ASD							
Frontal							
IFG	L	200	-44	20	24	4.31	4.31
[a]	L	[a]	-54	26	14	3.30	3.30
IFG (opercularis)	L	[a]	-52	12	20	4.03	4.03
Temporal							
Heschl's gyrus	R	4242	50	-14	6	13.46	7.45
[a]	R	[a]	42	-22	10	10.72	6.71
STS	R	[a]	52	-12	-6	9.39	6.26
[a]	R	[a]	66	-28	10	9.30	6.23
[a]	R	[a]	54	-26	10	8.36	5.87
STS	L	4796	-44	-26	12	11.26	6.87
[a]	L	[a]	-54	-24	10	10.10	6.50
[a]	L	[a]	-48	-14	0	9.31	6.23
[a]	L	[a]	-64	-28	8	7.91	5.69
MTG	L	[a]	-62	-14	-4	7.90	5.68
Parietal							
Precuneus	R	138	24	-48	12	3.96	3.96
Limbic							
Hippocampus	R	261	20	-10	-18	5.26	5.26
[a]	R	[a]	30	-12	-18	3.53	3.53
Amygdala	R	[a]	32	0	-20	3.48	3.48
	L	146	-20	-8	-16	4.46	4.46
Cerebellum							
Cerebellum lob crus 2	L	111	-18	-74	-40	4.66	4.66
NT							
Temporal-Parietal							
Heschl's gyrus	R	3010	50	-14	6	10.63	6.68
STS	R	[a]	62	-16	-2	9.86	6.43
[a]	R	[a]	58	-2	-2	7.06	5.31
[a]	R	[a]	54	-30	6	6.76	5.16
aSTS	R	[a]	62	4	-10	7.87	5.67
MTG	L	3867	-62	-32	6	9.84	6.42
[a]	L	[a]	-54	-22	0	9.49	6.30
STS	L	[a]	-62	-20	6	9.55	6.32
[a]	L	[a]	-52	-6	-6	7.96	5.71
Heschl's gyrus	L	[a]	-38	-30	14	8.57	5.96
Temporal							
IFG	L	184	-44	-40	-20	5.51	4.49
ITG	L	[a]	-36	-36	-14	3.97	3.51

Note. We show *t*-values for signal increases for the average effect of neutral stories (NEUT) in autism (ASD) and neurotypical (NT) control group. No clusters survive in between-group comparisons. Laterality (Lat), right (R) or left (L), number of voxels in each cluster (Voxel), XYZ coordinates, *t*-values and *z*-scores. Coordinates are MNI space. Height threshold $t = 3.41$, $p < .001$ cluster corrected.
[a] Subpeaks of larger cluster immediately above.

Appendix I: Brain-behavior correlation tables, Study 2

Table 1

Brain-behavior correlations: TOM ROI and ASD (n = 14)

		Region of interest							
Cond	**Measure**	dmPFC	mPFC	Amyg	Prec	lTPJ	lSTS	rTPJ	rSTS
POS	IQ	-.101	.231	.277	.112	.370	.505	.273	.177
	WRAML	-.381	.056	.052	-.273	.423	.011	.650*	.271
	WJIII	-.340	.134	.312	-.152	.461	.471	.421	.399
	M in E	.230	.310	.581*	.170	.128	.487	-.173	.045
	AQ	.067	-.389	-.606*	-.126	.112	-.084	.217	.068
	EQ	.022	.640*	.681**	.337	.166	.410	.086	.027
	SCQ	.000	-.048	-.357	-.041	-.005	-.091	-.025	.121
	STAIT	-.243	-.237	-.030	.102	-.174	-.276	.090	-.001
	TAS-20	.131	-.479	-.469	-.079	-.131	-.369	.413	.146
	ADOS-C	.218	-.293	-.045	-.440	-.433	-.071	-.257	-.065
	ADOS-S	.481	-.343	-.272	-.227	-.178	.059	.016	.282
	ADOS-CM	.408	-.347	-.199	-.329	-.294	.010	-.094	.161
NEG	IQ	-.272	-.393	.029	-.431	-.303	.399	-.120	.049
	WRAML	-.378	.011	-.185	-.300	.313	-.121	.481	-.063
	WJIII	-.356	-.266	-.077	-.457	-.106	.250	-.008	.198
	M in E	.303	-.248	.207	-.250	-.306	.454	-.497	-.055
	AQ	-.286	.046	-.218	.006	.122	-.092	.437	.132
	EQ	.108	-.218	.160	-.108	-.157	.360	-.217	-.264
	SCQ	-.207	.091	-.327	.222	.179	.039	.253	.278
	STAIT	-.103	.228	.426	.129	.011	-.337	.205	-.093
	TAS-20	-.210	-.038	-.206	.090	.090	-.470	.498	-.144
	ADOS-C	.334	-.157	-.364	-.235	-.138	-.072	-.103	-.167
	ADOS-S	.150	-.230	-.495	-.048	-.033	.026	.194	.034
	ADOS-CM	.235	-.216	-.477	-.127	-.078	-.012	.087	-.045
NEUT	IQ	-.300	-.369	-.025	-.417	-.240	.365	-.049	.022
	WRAML	-.402	-.149	-.015	-.497	-.079	.095	.325	.035
	WJIII	-.366	-.259	-.099	-.453	-.083	.242	.021	.191
	M in E	.287	-.208	.147	-.226	-.201	.409	-.446	-.096
	AQ	-.286	.044	-.222	.003	.137	-.091	.469	.136
	EQ	.122	-.248	.203	-.125	-.279	.419	-.291	-.251
	SCQ	-.210	.095	-.342	.225	.225	.038	.279	.280
	STAIT	-.119	.262	.409	.150	.109	-.400	.284	-.114
	TAS-20	-.188	-.101	-.137	.055	-.097	-.419	.436	-.109
	ADOS-C	.346	-.176	-.358	-.248	-.224	-.051	-.146	-.158
	ADOS-S	.171	-.270	-.476	-.070	-.154	.079	.145	.058
	ADOS-CM	.254	-.250	-.461	-.147	-.193	.031	.036	-.026

Note. Autism group (ASD) brain-behavior correlations for positive (POS), negative (NEG) and neutral (NEUT) conditions (Cond) for TOM regions of interest: dmPFC, dorsal medial prefrontal cortex; mPFC, medial prefrontal cortex; Amyg, amygdala; l, left; Prec, precuneus; r, right; STS, left superior temporal sulcus; TPJ, temporal parietal junction. Assessments (Measure): IQ, Full scores from the Wechsler Abbreviated Intelligence Scales (WASI) or Wechsler Adult Intelligence Scales (WAIS); WRAML, Wide Range Assessment of Memory and Learning age-adjusted scaled scores (Rutter, Bailey & Lord, 2003); WJIII, Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock et al., 2001); AQ, Autism Spectrum Quotient

(Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001); SCQ, Social Communication Questionnaire (Rutter, Bailey, & Lord, 2003); EQ, Empathy Quotient (Baron-Cohen & Wheelwright, 2004); M in E, Reading the Mind in the Eyes-Revised (Baron-Cohen, Wheelwright, Hill, et al., 2001); TAS-20, Toronto Alexithymia Scales (Bagby, Parker, et al., 1994; Bagby, Taylor, et al., 1994); STAIT, State Trait Anxiety Inventory (Spielberger, 2010); ADOS, Autism Diagnostic Interview-Revised (Lord et al., 2000); ADOS-C, communication scores; ADOS-S, social scores; ADOS-CM, combined communication and social scores.
*$p < 0.05$, **$p < 0.01$

Table 2

Brain-behavior correlations: TOM ROI and NT (n = 16)

		Region of interest							
Cond	**Measure**	dmPFC	mPFC	Amyg	Prec	lTPJ	lSTS	rTPJ	rSTS
POS	IQ	-.310	.047	.283	-.133	.023	.197	-.526*	.306
	WRAML	.160	.452	-.003	.252	.185	.317	-.226	.652**
	WJIII	.127	.356	.535*	.067	.318	.271	-.302	.294
	M in E	.005	.287	.257	.136	-.082	.330	-.297	.502*
	AQ	.083	-.231	-.102	-.163	.440	.231	.394	-.080
	EQ	.206	.568*	-.014	.205	.062	.221	-.145	.645**
	SCQ	-.155	-.480	.040	-.023	.047	.038	.177	-.352
	STAIT	.085	-.068	-.151	-.209	.160	.214	.453	-.049
	TAS-20	-.119	-.118	-.360	.315	-.137	.030	.228	-.046
NEG	IQ	-.367	.079	.034	-.113	-.168	.178	-.288	.324
	WRAML	-.026	.093	-.103	-.103	-.060	.147	-.290	.452
	WJIII	.081	.327	.241	.190	.201	.269	.019	.344
	M in E	.080	.398	.003	.125	-.116	.333	.028	.491
	AQ	-.063	-.313	.032	-.339	.406	.225	.152	.008
	EQ	.174	.212	-.229	-.033	-.052	.061	-.015	.532*
	SCQ	-.161	-.298	.263	-.042	.181	.129	.114	-.192
	STAIT	-.146	-.212	-.204	-.413	.133	.210	.116	-.127
	TAS-20	-.258	-.420	-.059	-.148	-.127	-.017	-.200	-.155
NEUT	IQ	-.426	.125	.055	-.263	-.211	.094	-.345	.056
	WRAML	-.121	.091	-.130	-.317	-.157	.035	-.362	.101
	WJIII	.019	.359	.301	-.061	.034	.126	-.154	.041
	M in E	-.105	.115	.002	-.184	-.381	.202	-.433	.132
	AQ	-.212	-.518*	-.037	-.481	-.013	.072	-.180	-.101
	EQ	.080	.263	-.209	-.169	.064	.049	-.048	.354
	SCQ	-.221	-.436	.179	-.090	-.184	.076	-.090	-.232
	STAIT	-.022	-.364	.015	-.221	.040	.252	-.044	.183
	TAS-20	-.187	-.383	-.057	.032	-.108	.103	.028	.021

Note. Neurotypical group (NT) brain-behavior correlations for positive (POS), negative (NEG) and neutral (NEUT) conditions (Cond) for TOM regions of interest: dmPFC, dorsal medial prefrontal cortex; mPFC, medial prefrontal cortex; Amyg, amygdala; l, left; Prec, precuneus; r, right; STS, left superior temporal sulcus; TPJ, temporal parietal junction. Assessments (Measure): IQ, Full scores from the Wechsler Abbreviated Intelligence Scales (WASI) or Wechsler Adult Intelligence Scales (WAIS); WRAML, Wide Range Assessment of Memory and Learning age-adjusted scaled scores (Rutter, Bailey & Lord, 2003); WJIII, Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock et al., 2001); AQ, Autism Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001); SCQ, Social Communication Questionnaire (Rutter, Bailey, & Lord, 2003); EQ, Empathy Quotient (Baron-Cohen & Wheelwright, 2004); M in E, Reading the Mind in the Eyes-Revised (Baron-Cohen, Wheelwright, Hill, et al., 2001); TAS-20, Toronto Alexithymia Scales (Bagby, Parker, et al., 1994; Bagby, Taylor, et al., 1994); STAIT, State Trait Anxiety Inventory (Spielberger, 2010).
*$p < 0.05$, **$p < 0.01$

Glossary

a. anterior

aCC. anterior cingulate cortex

ADOS-R. Autism Diagnostic Observational Scale - Revised

ANOVA. analysis of variance

ASD. autism spectrum disorder

aSTS. anterior superior temporal sulci

aTP. anterior temporal pole

AQ. Autism Quotient

ART. artifact detection tool

b. bilateral

BOLD. blood oxygenated level dependent

CC. cingulate cortex

CON. congruent

d. dorsal

db. decibel

dl. dorsolateral

dmPFC. dorsal medial prefrontal cortex

EB. multiband

EIT. Emotional Inference Task

EMO. emotional

EPI. echo planar imaging

EQ. Empathy Quotient

IFG. inferior frontal gyrus

INCON. incongruent

IPL. inferior parietal lobe

***F*.** *F*-statistic

FIR. finite impulse response

fMRI. functional magnetic resonance imaging

FOV. field of view

FWE. family-wise error rate

FWHM. full width half maximum

F0. frequency

GLM. general linear model

l. left

L. left

Lat. laterality

LH. left hemisphere

Lob. lobule

m. medial

M. middle

***M*.** mean

mm. millimeter

mCC. medial cingulate cortex

MNI. Montreal Neurological Institute

mPFC. medial prefrontal cortex

MPRAGE. magnetized-prepared, rapid gradient-echo

msec. millisecond

MVPA. multivoxel pattern analysis

MTG. middle temporal gyrus

***n*.** sample size

NARR. narrative ROI map

NEG. negative

NegCon. negative congruent

NegIncon. negative incongruent

NEUT. neutral

NeutCon. neutral congruent

NeutIncon. neutral incongruent

NT. neurotypical

Occ. occipital

op. opercularis

p. posterior

***p*.** *p*-value

PC. precuneus

pCC. posterior cingulate cortex

POS. positive

PosCon. positive congruent

PosIncon. positive incongruent

pSTS. posterior superior temporal sulci

QOL. quality of life

r. right

R. right

RH. right hemisphere

RM. repeated measures

ROI. region of interest

RT. response time

SCQ. Social Communication Questionnaire

SE. standard error

SD. standard deviation

SMA. supplemental motor area

SMG. secondary somatosensory regions

SPM12. Statistical Parametric Mapping

STAIT. State Trait Anxiety Inventory

STG. superior temporal gyrus

STS. superior temporal sulcus

t. *t*-score

T/F. true/false

TAS-20. Toronto Alexithymia Scale (20-item)

ToM. Theory of Mind

TOM. theory of mind ROI map

TPJ. temporal parietal junction

tri. triangularis

v. ventral

vmPFC. ventromedial prefrontal cortex

WAIS. Wechsler Adult Intelligence Scale

WASI. Wechsler Abbreviated Scale of Intelligence

WRAML-2. Wide Range Assessment of Memory and Learning

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Inferring Emotion from Language

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ABSTRACT

A fundamental aspect of successful social interactions is the ability to quickly and accurately comprehend the implied meaning of others' verbal messages, an ability requiring that the listener draw inferences often related to how the speaker feels. The objective of this study was to examine the neural correlates of language processing specifically related to emotional messages that require inferencing using functional magnetic resonance imaging (fMRI). For example, hearing "*My bike was stolen*" suggests that the speaker is unhappy, or angry. Participants (*n*=22) listened to short vignettes describing a protagonist's emotional state (positive, negative or neutral), then responded to a true or false decision. Changes in the BOLD contrast were analyzed separately for the story and the response period. Consistent with previous studies, emotional conditions elicited areas of activation in medial and orbital frontal regions as well as bilateral middle temporal areas, temporal parietal junction/superior temporal gyri and precuneus/cingulate cortex, regions that have been associated with both the processing of affective stimuli as well as social cognition in general. Moreover, these regions responded differentially to stimuli with either positive or negative valence, especially in the medial prefrontal cortex (mPFC), where negative stories elicited more dorsal mPFC and positive stories elicited more ventral mPFC. We additionally found that activity in regions typically associated with belief representation (mPFC, anterior temporal lobes, and temporal/parietal junction) was significantly greater for emotional stories compared to neutral, demonstrating a role of these regions in making inferences about others' emotional states beyond belief representation. Finally, contrary to previous research on

emotional inferencing, we did not find subcortical activity in the amygdala and striatum during the story phase. However, this subcortical activation was exhibited in the context of the true/false congruency judgment, including the putamen, caudate, insula and amygdala, suggesting that previous findings may be due to decision-making factors on emotion.

INTRODUCTION

The study of language comprehension or discourse processing has generally focused on the ability to extract meaning from language (spoken or written) and connect it to our extant knowledge of the world and how it works (Barsalou, Santos, Simmons, & Wilson, 2008; Kintsch, 1998; Walter Kintsch & Dijk, 1978). This process entails drawing inferences about content not explicitly stated, but rather dependent on schemas activated from prior knowledge and our ability to access them. One specific aspect of discourse that is often implied, but not stated explicitly, is the affective context of the actors in a story, or of conversational partners. When a listener of a story hears about a particular event (e.g., a house fire), they are often left to infer how the actors in the story feel. These types of bridging inferences are elaborations on the information directly presented and, from a psycholinguistic perspective, are not obligatory or necessary to maintain the coherence of a story (Graesser, Singer, & Trabasso, 1994). Moreover, inferences involving human actors involve social processes of mentalizing or Theory of Mind (ToM), in which the listener may more readily construct a situation model representation of the discourse. In such cases, it is argued that the listener engages “a mental model of the situation” including the social-emotional processes that would be evoked by the actor(s) in the story (Wellman, Cross, & Watson, 2001). As such, the processes involved in drawing such inferences may go beyond the simple linguistic/semantic and perceptual systems engaged in building such a representation to include emotion and ToM. The fundamental research question posed here is

whether neural systems engaged when inferring an actor's emotional state differ compared to physical states such as energetic or fatigued.

Overall, the majority of findings on narrative comprehension reveal activation of medial frontal and bilateral temporal and parietal regions (Ferstl & Neumann, 2008; Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mar, 2004, 2011; Prat, Mason, & Just, 2012). More specific investigations of the neurobiology of inferential processing have generally shown a consistent set of cortical regions which include: bilateral anterior temporal lobes (aSTS) extending to the superior temporal sulcus (STS), inferior frontal gyrus (IFG), medial prefrontal cortex (mPFC) and posterior cingulate cortex/precuneus (pCC/PC). This network is argued to be engaged when elaborating upon the linguistic information presented beyond processing syntax and maintaining coherence, such as elaborative, bridging, or causal inferences (Jung-Beeman, 2005; Jung-Beeman et al., 2004; Tyler & Marslen-Wilson, 2008; Virtue, Haberman, Clancy, Parrish, & Jung Beeman, 2006). Additionally, discourse involving human characters invokes ToM processes, or the ability to attribute mental states (e.g., beliefs or desires) to others and use this information to explain or predict their actions, motivations, intentions, etc. (Ferstl & von Cramon, 2002; Mar & Oatley, 2008). Brain regions typically involved in story-based ToM processing include mPFC, pCC/PC, and bilateral aSTS and pSTS (Frith & Frith, 2003; Gallagher & Frith, 2003; Saxe & Kanwisher, 2003; Saxe & Powell, 2006). While this network (which overlaps with the putative "default mode network"; Spreng & Grady, 2009) is generally associated with mentalizing, functional divisions arise depending on the type of mental state attribution. Specifically, bilateral TPJ respond more to stories requiring representation of a character's thoughts than their physical description or enduring personality traits (Heberlein & Saxe, 2005) or to physical pain of that

character (Bruneau, Pluta, & Saxe, 2012). Midline structures (mPFC and pCC/PC), however, are associated both with judgments about the transient contents of one's mind (e.g., thoughts and beliefs) as well as enduring personality traits or physical characteristics of the self and other (Mitchell, Macrae, & Banaji, 2006; Moran, Lee, & Gabrieli, 2011). What is apparent is that there is overlap in the cognitive and neural mechanisms for narrative comprehension and mentalizing (Mar & Oatley, 2008; Mar, 2011).

During verbal communication, knowledge or understanding of the speaker's emotions are made both from explicit emotional statements (e.g., "*I am mad at my teacher*") as well as language that implies an emotion or an emotion may be inferred (e.g., "*I got a new bike for my birthday*"). However, the majority of investigations of emotional language have employed arousing or valent words in isolation, thus eliminating the need for inferencing (see Citron, 2012 for review). Recent studies suggest that processing single affective words engages brain areas associated with emotion. For example, the amygdala is activated in response to both highly negative (Isenberg et al., 1999; Kensinger & Schacter, 2006; Maddock & Buonocore, 1997; Maddock, Garrett, & Buonocore, 2003; Maratos, Dolan, Morris, Henson, & Rugg, 2001; Nakic, Smith, Busis, Vythilingam, & Blair, 2006; Tabert, Borod, Tang, & Lange, 2001) as well as positive words (Briesemeister, Kuchinke, Jacobs, & Braun, 2014; Hamann & Mao, 2002; Harenski & Hamann, 2006; Kensinger & Schacter, 2006; Maddock et al., 2003). Additionally, both positive and negative words evoke activations in medial/orbital PFC and cingulate cortex (Beauregard et al., 1997; Maddock et al., 2003; Maratos et al., 2001). However, emotionally arousing words—especially in isolation—do not reflect every day social discourse. Instead, verbal interactions typically consist of narratives that frequently connote mild and/or mixed emotions, and often

require the listener to *infer* the feeling of the speaker. For example, if a listener hears, "*Frank worked all night on his essay, but his computer crashed and he lost his work*," it is immediately understood to involve negative emotions, e.g., distress or frustration.

Whereas the literature on mentalizing and emotion are quite robust, neuroimaging studies of affective semantics at the sentence and story level are less prevalent. One report showed that listening to short emotional sentences spoken by both actors and machines (lacking prosody) recruited two general networks: 1) bilateral IFG, bilateral anterior insula, pre-supplementary motor area (SMA) as well as subcortical areas (left thalamus and right caudate nucleus), and 2) dorsal medial (dm)PFC and left pSTS (Beaucousin et al., 2007). Another study employed longer emotional scenarios (~45sec) with embedded inconsistencies. When the inconsistency concerned emotion, activations were revealed in ventromedial (vm)PFC, dorsal PC and left amygdaloid complex (Ferstl, Rinck, & von Cramon, 2005). Most social interactions, however, are not characterized by lengthy monologues. An investigation (Ferstl & von Cramon, 2007) using very short visually-presented emotional scenarios showed that aSTS, but not vmPFC or amygdala, was sensitive to the emotional content of the scenario. The authors suggested that the lack of response in medial structures may have been due to shallower processing of the short stimuli.

The bulk of the literature on inferring emotional states of others has generally been in comparison with other constructs of mentalizing (e.g., false beliefs, strategic thinking, intentions) to support specific representational models of ToM processing (Corradi-Dell'Acqua, Hofstetter, & Vuilleumier, 2014; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). For instance, Mason and colleagues (2008) compared stories requiring an inference about a character's intentions or

emotional state and found rTPJ activation for intentions but not emotions. Similarly, Corradi-Dell'Acqua and colleagues (2014) demonstrated in a univariate analysis selective engagement of bilateral TPJ and pCC/PC when listening to stories about other's beliefs but not their emotions. The vmPFC was responsive to both belief and emotion stories. However, they found equivalent activation within these regions when making *judgments* about a character's belief or emotion. Moreover, they found high correlations between beliefs and emotion across the ToM network when using a multivoxel pattern analysis (MVPA) approach. Variations between analytic approaches were also seen for Zaitchik and colleagues (2011) who found greater activation for mentalizing (belief/representation) relative to emotion in bilateral STS and IPL in an region of interest (ROI) analysis when adding mental state words (e.g. "thought", "remember") to the emotional sentences. In contrast to these past studies, several studies have shown no differences in the general ToM network between emotion and belief stories (Bruneau et al., 2012; Hynes, Baird, & Grafton, 2006). Hynes and colleagues (2006) found no differences comparing cognitive perspective taking and emotion perspective taking in the general ToM network (rTPJ, bilateral STS, dmPFC, mPFC), but observed some variation in lateral orbital frontal cortex and IFG. Bruneau and colleagues (2012) asked participants to (1) rate the amount of pain felt by protagonists, or (2) actively empathize with the protagonist in stories of physical pain, emotional pain, or false beliefs and compared activation to matched control stories. They found generally similar patterns across tasks with greater activation in bilateral TPJ for empathizing. Importantly, they found that while emotional pain and false beliefs similarly activated the ToM network, physical pain stories activated an "empathy network" including insula, secondary sensory (supramarginal gyrus), middle frontal, and mid aCC all bilaterally (Decety & Lamm, 2007; Fan, Duncan, de Greck, & Northoff, 2011; Lamm, Decety, & Singer, 2011). Variation between

emotional pain and physical pain was explored further by Bruneau and colleagues (2013) who analyzed cortical response to the same stories using an item-level regression approach with ratings of emotional pain, physical pain and vividness. Again, ratings of physical pain correlated with activation in the empathy network, whereas emotional pain correlated with activation in the dorsal and ventral aspects of the mPFC and the pCC/PC region. In short, it is unclear how unique the neural network for understanding emotion is from other aspects of mentalizing and these effects may be partially driven by analytic method.

In findings discussed above, the degree to which the individual has to “infer” the emotion of the protagonist is confounded by several factors. In each of the studies above, the scenarios used explicitly mention the emotional state of the protagonist or combined story and judgment in the analyses eliminating the need for inferential processes with the exception of Corradi-Dell’Acqua et al. (2014) and Bruneau et al. (2012). However, the latter two studies include mental or other (non-target) emotional state words. As such, the patterns of activation seen in these studies could equally reflect the response to emotion or mental state words without providing much insight into inferential process what a protagonist is experiencing. Furthermore, the previous studies have generally included a behavioral response specific to the emotion or mental state in the window of analysis (Beaucousin et al., 2007; Ferstl & von Cramon, 2007; Hynes et al., 2006; Zaitchik et al., 2011) with the exception of a few which separated the response period (Corradi-Dell’Acqua et al., 2014) or contained an unrelated response (e.g., respond when finished reading, Saxe & Powell, 2006). The inclusion of a response specific to the mental state/emotion may similarly engage regions artificially and not reflect a pure inferential process. For instance, it may be the case that activation of the amygdala is a product of such decision responses to

affective stimuli as has been shown with viewing faces with affect (Pérez-Edgar et al., 2007), and may not be a product of the inferential process.

In summary, the literature on processing emotion from language has been limited to explicit references of emotion words either in the target statements (e.g., Corradi-Dell'Acqua et al., 2014; Zaitchik et al., 2011) or in a decision making component (Beaucousin et al., 2007; Ferstl & von Cramon, 2007; Zaitchik et al., 2011). Thus, it remains unclear what neural mechanisms are involved when one must actually infer the emotional state of others from situational contexts as described in language as opposed to explicitly being made aware of them. The question posed in our study is whether affective verbal utterances—lacking explicit lexical references of emotion and therefore necessitating inference—would recruit only regions associated with discourse processing or additional regions associated with mental state or emotional processing.

PRESENT STUDY

The aim of this investigation was to identify the underlying network of cortical regions involved in making inferences of affect from spoken discourse context. To achieve this goal, positive, negative and neutral scenarios (with natural but unaffected prosody) were presented to healthy participants during functional magnetic resonance imaging (fMRI). During the scan, subjects listened to the scenario then made a true-false (T/F) congruency judgment related to the emotion of the protagonist. Changes in the Blood Oxygenated Level Dependent (BOLD) contrast were analyzed on two periods: 1) listening to the scenario, and 2) response period. While previous research has examined neural activations associated with emotional inferencing at the sentence/discourse level, to our knowledge this is the first to identify the effects of positive and negative scenarios separately and which avoids the confound of explicit labels of emotion.

With respect to language processing systems in the brain, we hypothesized that listening to stories in all three conditions would elicit activations in regions involved in language comprehension, namely activation of mPFC along with bilateral temporal and parietal regions (Ferstl & Neumann, 2008; Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mar, 2004; Prat, Mason, & Just, 2012) as well as regions of the ToM network, including mPFC, pCC/PC, and bilateral aSTS and pSTS. Additionally, given the previous findings of Ferstl and von Cramon (2005) as well as selected single word studies (Kensinger & Schacter, 2006; Maddock et al., 2003; Straube et al., 2011), we expected that emotional scenarios would involve areas consistent with processing emotions, i.e., bilateral amygdala, cingulate, and orbitofrontal cortices (reviews: Dolan, 2002; Phillips, Drevets, Rauch, & Lane, 2003; Wager, Phan, Liberzon, & Taylor, 2003). However, by temporally separating the cortical response to our decision from the story phase we can determine whether particular structures such as the amygdala are involved in the online inferential processing of emotion from the scenarios or if it is activated as a result of the decision-making process in which reference to emotion is explicit. Because all of our scenarios involve reflecting on the experience of a protagonist, we assume that all conditions involve some degree of social processing. Thus, the resulting differences between conditions will reflect the influence of affect in the inferential process. Given previous behavioral research on affective word processing (Herrington et al., 2005; Kuchinke et al., 2005; Straube et al., 2011), we predicted that the positive scenarios would evoke faster responses than the negative (compared to neutral).

METHODS

PARTICIPANTS

Twenty-two native English speakers recruited from the greater Washington DC area contributed data to the present study (11M; mean age 21.3). Data from two individuals (and one run from one participant) were excluded due to low accuracy resulting in a final sample size of 20. All subjects reported being free of auditory deficits, neurological and major medical conditions, and had no history of head trauma (loss of consciousness of more than ten minutes and/or head injury). Participants also reported that they had no history of any substance dependence and were not currently medicated.

All participants completed the Edinburgh Handedness Inventory (Oldfield, 1971), and received behavioral assessments including the Oral Language Comprehension (test 15) from the Woodcock Johnson III Ability Tests (Woodcock, McGrew, & Mather, 2001), and two measures designed to identify the presence and extent of autistic symptomatology: the Autism Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) and the Social Responsiveness Scale (Ingersoll, Hopwood, Wainer, & Brent Donnellan, 2011), as future plans include extending this paradigm to autistic individuals. All study participants received a thorough explanation of the experimental procedures, and written consent was obtained in accordance with the requirements of the Institutional Review Board of University of Maryland. Subjects received monetary compensation.

STIMULI

Sentence Construction and Selection

The initial corpus was composed of 108 scenarios (36 each negative, positive, and physical state for the neutral condition, see Table 1 for sample stories). The stories were constructed such that the information related to the feeling- or physical state appeared as close to the beginning as possible. All sentences were consistent with a target response, "He/she felt *xxx*." Emotional sentences were designed to use words selected from Mind Reading software (Simon Baron-Cohen & Wheelwright, 2004) a program that includes over 400 emotion words; target words chosen were rated as familiar to > 95% of 15-16 year olds (Simon Baron-Cohen, Golan, Wheelwright, Granader, & Hill, 2010). Words forming the basis of the neutral target sentences related to a bodily state or physical condition and lacking an emotional dimension in the sentential context. See Supplemental Materials (Table S1) for target words for all scenarios. Passages were recorded by an adult female using PRAAT recording software (pitch range 100-500 Hz, sampling frequency 44100 Hz, mono signal) (Boersma, 2001). Initial recordings were normalized for intensity by calculating the average of all files (72.45 db total, range 67.81 to 77.15) and scaling all recordings to this average. To verify the absence of prosodic cues, an acoustic analysis was conducted to evaluate the utterances on the activation dimension (high vs. low energy) using PRAAT software (Boersma & Weenink, 2004). Particular attention was paid to F0, the main parameter reflecting emotion in prosody, with negative emotions characterized by a low, monotonous F0 pattern and positive emotions by higher, more wide-ranging F0 (Bänziger & Scherer, 2005; Scherer, 1986). Single factor analysis of variance failed to reveal differences between conditions for either mean F0 (ANOVA; $F(2,69) = .68$, $p = > .05$) or F0

range (ANOVA; $F(2,69) = 1.63$, $p = > .05$). The stories had an average duration of 11.02 sec (range 9.74-11.74 sec).

A separate set of participants were used to normalize the stimulus. Nineteen typically developing adults (11 F; 18.1-22.5 years of age) recruited from the University of Maryland performed a cloze task procedure to assess the precision of the contexts in evoking particular emotional states and also rated stories for valence and familiarity. The criteria used included: a) positive and negative scenarios were deemed appropriate if they received 100% agreement from all participants (target word or a synonym), b) physical state stories were deemed accurate if the response was consistent with the physical state *or* a neutral emotion was supplied, e.g., "satisfied." Furthermore, among those stories meeting the consistency criteria, those judged to have highest (for positive), lowest (for negative) and most neutral (for physical state) valence ratings were selected. Valence ratings were collected on a scale of -3 to +3, with -3 being most negative and +3 most positive. From the norming results, the average valence for negative stories = -2.48, positive stories = 2.52, and neutral stories = -1.80. In total, 72 stories were chosen, 24 in each condition. For the fMRI paradigm, congruent and incongruent response conditions were created for each of the scenarios in the form of a true-false statement, for example, “She felt happy.” See Supplemental Materials for complete norming results and corpus of stimuli.

TASK PROCEDURES

Trial structure of the Emotional Inference Task (EIT) is presented in Figure 1. A total of 72 passages with 24 positive, 24 negative and 24 neutral trials and a congruent and incongruent

Target sentence for each were evenly distributed over four runs using an event-related paradigm. The congruent and incongruent items were randomized such that each participant received 12 congruent and 12 incongruent Target sentences per condition. Each run began with the display of a fixation cross for 500msec, followed by the aurally-presented passage (~10-12sec). A blank screen followed for a duration jittered between 3-6 seconds. Then, the target sentence stating "He/She felt…" with a congruent or incongruent word was presented visually for 3sec during which a true or false congruency judgment was made via a button press. Each trial (from Cue to Target sentence) was presented for 16-18sec, inter-trial interval was jittered 3-5sec. Participants were instructed to listen carefully to each scenario, and think about the feelings of the protagonist. They were told that they would then see a short sentence, to which they would respond "true" or "false" by pressing a button on the response box. The tasks were implemented with MATLAB version 2010b (MATLAB, 2010), using Psychophysics Toolbox (Brainard, 1997).

ACQUISITION OF FUNCTIONAL MR DATA

Subjects were scanned using a Siemens 3T Trio MRI system with a 32-channel head coil. Functional images to estimate task-related activity were obtained with a gradient echo-planar imaging (EPI) sequence (repetition time=2000 msec, echo time=2400 msec, 64 × 64 matrix, flip angle 70°, FOV 192 mm). Whole brain coverage was obtained with 36 axial slices (thickness=3.2 mm; in-plane resolution=3.0 × 3.0 mm). A high-resolution T1-weighted MPRAGE scan (repetition time=1900 msec, echo time=2320 msec; field of view=230 mm; flip angle=9°; 192 sagittal slices; thickness=0.9 mm; 0.9 × 0.9 matrix) was obtained covering the whole brain.

DATA ANALYSIS

Analysis of Behavioral Data

Performance measures were accuracy and response time (calculated on correct trials only) to the EIT Target sentence recorded during fMRI acquisition. We examined the effect of valence and congruency on accuracy and response time separately with a two (group: congruent, incongruent) by three (valence: positive, negative, neutral) repeated measures analysis of variance (ANOVA). Post-hoc pairwise comparisons were Bonferroni corrected. Statistical analyses of behavioral data were performed using IBM SPSS (version 21.0).

Analysis of Functional MR Data

Data analysis was performed using Statistical Parametric Mapping (SPM12b, http://www.fil.ion.ucl.ac.uk/spm). Preprocessing of the EPI time series included: (1) realignment for head motion correction, (2) spatial normalization into the Montreal Neurological Institute (MNI) anatomical space, and (3) spatial smoothing (6mm FWHM). Data were high pass filtered at 128 Hz, and examined for excessive motion and spiking artifacts using the Artifact Detection Tool (ART) software package. Outliers in the image time series (Z-threshold: 3.0, scan to scan movement threshold 1.0 mm) were identified and excluded from subsequent statistical analysis (4.6% of the data).

For each participant, a general linear model (GLM) was used to estimate the parameters for the stories and probe separately. The story model included three story factors: positive (“POS”), negative (“NEG”), and neutral (“NEUT”) as well as a factor for each of the two probe conditions, congruent and incongruent. In order to evaluate the effect of response time (RT), an

additional model including individual RT times as a parametric modulator for each of the probe conditions was employed. All factors were convolved with a canonical hemodynamic response function (Friston, Frith, Turner, & Frackowiak, 1995). Six realignment parameters as well as outlier time points were included in the models as regressors of no interest. The contrast images from the first level analyses were then subjected to second level random effects analyses.

To determine regions of increased task-related signal change for the overall effect of listening to stories (POS+NEG+NEUT) relative to the implicit (fixation) baseline at the group level, we performed a one-way ANOVA and reported the overall effects of condition. To examine the effect of valence, whole brain analysis of stories was performed using a within subjects repeated measures design. The main contrasts of interest were the effect of emotion compared to neutral (POS+NEG>NEUT) as well as the individual contributions of NEG>NEUT and POS>NEUT. Effects of valence were further measured by comparing POS>NEG and NEG>POS.

Whole brain analysis of the probe was performed using *t*-tests for the event-related response to the congruent and incongruent conditions. An additional first-level model was conducted using item-level RT as a parametric modulator for condition effects on the probe (Grinband et al., 2011). As a factor, RT did not account for any activation in cortex. There was little difference in activation patterns with the addition of RT compared to the original, thus the analyses reported are those without the modulator. As behavioral results did not reveal statistically significant differences between conditions of valence, the main contrasts of interest were congruent and incongruent items separately. Whole brain contrasts were corrected at FWE $p < 0.05$.

RESULTS

Behavioral Results

A two (congruent, incongruent) x three (positive, negative, neutral) repeated measures ANOVA for response times to correct trials (RT) revealed a significant main effect for valence $F(1.444, 27.431)=30.126$, $p<.001$. Contrasts revealed that RTs to POS stories $F(1, 19) = 52.193$, $p<.001$, $r=.86$, and NEG stories $F(1, 19) = 8.996$, $p=.007$, $r=.57$, were significantly faster than NEUT. There were no significant differences between RTs to POS and NEG stories. There was also a significant effect of congruency $F(1, 19) = 9.189$, $p=.007$. RTs were significantly longer for INCON than CON trials. Accuracy scores were also subjected to a factorial repeated-measures ANOVA. There was a significant main effect of valence $F(1.252, 23.796) = 4.01$, $p=.049$. Contrasts revealed that accuracy to POS $F(1, 19) = 7.168$, $p=.015$, $r=.52$, was significantly better than NEUT; no significant differences were revealed. See Table 2 (and bar graph in Supplements).

Functional MRI Results

Stories

The overall effect of processing verbal scenarios was determined by collapsing across positive, negative and neutral stories. As depicted in Figure 2A, the analysis revealed activation in left inferior frontal (triangularis) and both dorsal and ventral aspects of PFC. There were also broad areas of significant activity in both temporal lobes, extending from pSTG to the anterior temporal poles (aTP), and including bilateral IFG and right inferior temporal gyrus. In addition, significant activation was found in areas of the parietal lobe comprised of bilateral postcentral and right angular gyri and in the occipital cortex including right superior- and middle occipital

gyri and a cluster including cuneus and lingual gyrus on the left. Activation was also seen within right hippocampus, left middle cingulate and bilateral calcarine. The cerebellum showed extended bilateral activation. See Supplements for details.

Emotion

To examine the effect of emotion, we compared emotional stories (collapsing across positive and negative) to neutral stories (Table 3). As shown in Figure 2B, medial frontal areas (dmPFC, vmPFC and orbital frontal gyrus), pCC)/PC, bilateral angular and temporal gyri, and right inferior temporal gyrus had significantly greater activation for emotion relative to neutral stories. Interestingly, the analysis also revealed clusters of activation that were greater to neutral relative to emotional stories located in left inferior frontal gyrus (IFG; triangularis) and supramarginal gyrus. These activations are adjacent to, but isolated from areas activated by the stories in general (Figure 2A) and the neutral stories relative to the implicit baseline (Figure 2B in blue)[1]. Parameter estimates for the story conditions at these clusters revealed that the contrast is a result of deactivation of these regions to emotional stories (both positive and negative, see bar plots Figure 3).

Valence

To further investigate the effects of emotion, we examined the contribution of POS and NEG through whole brain contrasts comparing NEG>NEUT and POS>NEUT. NEG>NEUT revealed greater activity in both dmPFC and vmPFC, right IFG, and large extents of activation along the STS bilaterally encompassing the aTL, mid temporal cortex (STG and MTG) extending to the

[1] Note that right IFG also appears to be significant for neutral stories in Figure 3B, but does not appear in Table 4. This is due to the figure showing activation at an uncorrected voxel level threshold ($p<0.001$) but a cluster corrected threshold ($FWE<0.05$) whereas the table on included peaks with voxel-wise corrected thresholds ($FWE\ p<0.05$).

temporal parietal junction (TPJ) (including angular gyri). Similarly, POS>NEUT elicited activation along the STS bilaterally including the aTP, STG, MTG and peaks in left angular gyrus, pCC/PC and additionally in mPFC, where activation was greater compared to the NEG>NEUT contrast (see Figure 3 images). Table 4 presents results of individual contrasts from the repeated-measures ANOVA. As many of the areas sensitive to valence are overlapping, we extracted the intensity of activation in selected regions of interest described above. Figure 3 (surrounding graphs) shows that the effects of both positive and negative valence were quite similar, and were stronger than neutral valence in all regions. In a direct comparison of POS and NEG valence, the regions that survived corrected threshold were the MTG for NEG>POS and the pCC for POS>NEG.

The effects of NEUT stories contrasted with both NEG and POS was also examined using individual contrasts from the repeated measures ANOVA. These contrasts showed that NEUT>NEG stories revealed two left frontal peaks, superior orbital gyrus and IFG, as well as supramarginal gyrus. As discussed in the contrast of NEUT>POS+NEG, this effect is the result of deactivation to emotional stories. The comparison of NEUT>POS showed nearly identical peaks (to that of NEUT>NEG) in both superior orbital gyrus and IFG (Table 4).

Decision-Making Response

To investigate the regions associated with the T/F decision we calculated a one-sample *t*-test for the response to the congruent and incongruent conditions. Individual response times were added as a covariate to explore the effect of RT. As these results were not significant, we suggest that the effects can be attributed to the condition of congruency and not to task difficulty. Several areas were activated for both the congruent and incongruent conditions (compared to baseline), including left- aSTS,

inferior temporal gyrus, angular gyrus, and right insula. Common bilateral activations were found in IFG, putamen, occipital lobe and cerebellum. Additional significant peaks related to the congruent condition included right- aSTS, and left- MTG, Heschl's gyrus, postcentral gyrus, insula and thalamus. Peaks of significant activation for the incongruent condition included superior frontal gyrus, right MTG, as well as bilateral amygdala, right caudate and left hippocampus (Figure 5; coordinate table in Supplemental materials).

DISCUSSION

Our aim was to understand the neural mechanisms supporting emotional inferences made from discourse context without direct references of emotion from verbal ("sad, happy, and mad") or non-verbal (prosody, facial expression) cues. To do this, we used vignettes devoid of overt emotional words or prosody, such that listeners were required to infer the protagonist's emotion using linguistic information only. Although previous studies have examined the neural correlates related to inferring emotion from language (Beaucousin et al., 2007; Corradi-Dell'Acqua et al., 2014; Ferstl et al., 2005; Ferstl & von Cramon, 2007; Mason, Williams, Kana, Minshew, & Just, 2008), to our knowledge this is the first to investigate the neural correlates related to processing scenarios of positive, negative and neutral valence separately without explicit use of emotion words. In addition, we analyzed the BOLD response to the verbal scenarios and response periods separately, allowing us to differentiate between neural activations during the period of inference from those concerned with explicit judgments of emotion or decision making in general.

Emotional Scenarios Evoke Activity in Areas Associated with Discourse, ToM, and Emotional Processing

Our primary hypothesis argued that emotionally valent stories would activate regions associated with emotional processing in addition to regions associated with discourse- and ToM processing

in general. Our findings revealed that the regions more responsive to emotional relative to neutral stories generally overlap with those activated by the neutral stories (see Figure 3B) suggesting that emotional stimuli enhances activation in areas responsive to discourse. This set of regions surrounding the mid-section of the STS bilaterally extending toward the temporal poles has been repeatedly shown to be engaged in narrative processing (Ferstl & Neumann, 2008; Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mar, 2004, 2011; Prat, Mason, & Just, 2012). As shown in meta-analyses of narrative processing (Ferstl & von Cramon, 2007; Mar, 2011), these regions are engaged irrespective of the inclusion of human characters or mentalizing processes in the stories themselves. These regions are also engaged whether the stories are presented auditorally or visually (Hickok & Poeppel, 2007; Jobard, Vigneau, Mazoyer, & Tzourio-Mazoyer, 2007), and for ToM processing whether story-based or not, as shown by Mar's (2011) meta-analyses (see Figure 5). Beyond the network associated with neutral stories, the emotionally valent stories elicited activation in medial and orbital PFC regions as well as bilateral STS/TPJ and pCC/PC. These findings are consistent with the hypothesis that inferring the emotional state of another engages regions associated with mentalizing (ToM), as all of these regions are part of the putative ToM network (Frith & Frith, 2003; Gallagher & Frith, 2003; Saxe & Kanwisher, 2003; Saxe & Powell, 2006).

Neutral Scenarios Engage Areas Responsive to Physical Sensations and Empathy

Contrary to our hypotheses, we did not find greater activation for emotional stimuli in the insula, dorsal aCC, or amygdala, regions traditionally associated with emotion processing and empathy (Decety & Lamm, 2007; Fan et al., 2011; Lamm et al., 2011). Instead, the contrast of NEUT<POS+NEG showed greater activation in IFG and supramarginal gyrus (SMG) bilaterally which tend to be associated with empathy for physical pain (Bruneau et al., 2013; Bruneau et al.,

2012) or bodily sensations (Saxe & Powell, 2006). Given the nature of the neutral stimuli which reflected more physical states of hunger, fatigue, or body temperature, the engagement of secondary somatosensory regions (SMG) and IFG regions just anterior to the insula suggests that these components of the empathy network are reflective of the physical, rather than emotional nature of the empathy response. Thus, our contrast of emotional relative to neutral stimuli reveals greater engagement of the network of regions associated with language and mentalizing, whereas the inverse contrast engages areas involved in empathy for physical sensations. Our findings are consistent with Saxe and Powell (2006), who showed the bilateral TPJ, within the mentalizing network, was activated for the processing of others mental states, but not their bodily sensations or appearance. The content of our neutral items included bodily sensations such a fatigue and hunger that may be more akin to their "non-mental" manipulations. This study extends these findings to demonstrate that inferences about emotional states (without reference to beliefs or desires) engage the TPJ to a greater extent than non-mental bodily states.

Narrative Processing or Mentalizing Networks?

Our theoretical aim was to determine whether drawing inferences regarding the emotion of another person is reflected in cortical regions beyond the language network. However, it is unclear exactly how unique the networks for language processing and mentalizing (Deen, Koldewyn, Kanwisher, & Saxe, 2015; Ferstl & von Cramon, 2001; Mar, 2011; Spreng & Mar, 2012). For instance, Figure 5 shows the spatial overlap in activation patterns reported in one meta-analysis conducted on studies of narrative processing (red) and studies of mentalizing or ToM in the context of stories (dark blue; Mar, 2011). The remarkable amount of overlap in the networks particularly along the STS (particularly, the TPJ and aTL), dorsal and ventral PFC and insula bilaterally suggests common underlying processes involved in these domains (Deen et al.,

2015; Redcay, 2008). Whereas some have suggested the common patterns of activation are indicative of processes of mental simulation of the thoughts and perspective of others (Mitchell, Banaji, & Macrae, 2005; Mitchell, 2009; however see Saxe, 2005), others have similarly argued that processes of retrospective and prospective memory that are required for understanding the goals and intentions of others are invoked (Buckner & Carroll, 2007; Schacter, Addis, & Buckner, 2007; Spreng & Grady, 2009; Spreng, Mar, & Kim, 2008) or that these networks reflect the control of cognition from externally modulated toward internal mental processes (Corbetta, Patel, & Shulman, 2008). It has also been argued that processes of ToM and narrative inferencing may independently activate a region such as mPFC (Ferstl & von Cramon, 2002) or that subnetworks such as a medial (mPFC and pCC system) modulate mental/emotional reactivity (Bruneau et al., 2013; Ochsner, Bunge, Gross, & Gabrieli, 2002), whereas the lateral network (bilateral TPJ) reflects a cognitive appraisal of the situation (Decety & Lamm, 2007; Mars et al., 2012). Despite the competing theories, it is necessary to determine the networks involved when actually inferring a protagonist's emotional state absent of the potentially confounding elements of explicit mental/emotional state words and task response. Whereas previous studies of emotional processing of scenarios have generally found engagement of the ToM network including bilateral TPJ, STS, and medial regions including dmPFC, vmPFC, and pCC/PC (Bruneau et al., 2012; Corradi-Dell'Acqua et al., 2014; Hynes et al., 2006; Zaitchik et al., 2011), most of these studies have focused on negative affect of painful experiences or did not account for the effects of valence.

Differential effects of Positive and Negative Scenarios

The direct comparisons of positive and negative valence at the stringent voxelwise correction revealed that negative stories produced greater activation in the left lateral MTG/STS region

whereas positive stories yielded greater activation in the mid/posterior cingulate region. However, comparison at a less stringent threshold ($p<.001$, FWE $p<.05$ cluster correction) reveals (Figure 6) a pattern in which negative stimuli more strongly activate the lateral temporal regions and the dorsal aspect of mPFC (Figure 3 in red) whereas positive stories are more associated with the pCC and ventral aspect of the mPFC. Specifically, there is a significant cluster in the ventral aspect of the medial orbital frontal area (xyz = -8, 60, -4) for positive versus negative stories, whereas the negative versus positive contrast reveals a cluster located more dorsally in the frontal superior medial region. These findings are consistent with a recent meta-analysis showing that the dorsal medial PFC is more active in response to negative feedback while the orbital/ventral PFC is more responsive to positive feedback and social acceptance (Crone, 2014). According to Crone, the connections to the dorsal mPFC from the dorsal anterior cingulate (daCC) and the supplementary motor area (SMA) serve as a negative feedback loop in social and cognitive functioning, whereas the ventral mPFC has more direct connections with the reward system in the subgenual aCC and ventral striatum and responds to positive social-affective feedback.

Moreover, the positive stories show greater activation in the posterior medial regions including the pCC/PC and neighboring posterior parietal and cuneus region in addition to the vmPFC region, which are associated with the ToM network shown in Figure 5. PCC activation across conditions revealed deactivation for neutral items and more positive activation for emotional items with positive stimuli being most active (see bar plot in Figure 3). As discussed, the pCC (in conjunction with the mPFC and TPJ) has been implicated as part of the brain’s default mode network (DMN) which is often shown as anti-correlated with task demands and the cognitive

control system (Fox et al., 2005). Based upon our behavioral results, it appears that our neutral condition was more difficult than the emotion conditions with respect to the EIT task and thus the pCC activity, and the similar pattern in vmPFC, could reflect effort in cognizing (the DMN explanation). On the other hand, the pCC has also been associated with the processing of pain and emotion (Maddock & Buonocore, 1997; Maddock et al., 2003), ToM (Saxe & Powell, 2006), and self-referential and other-referential processing (Spreng & Grady, 2009). Interestingly, meta-analyses reveal slight spatial variation in the pCC for investigations of memory relative to pain, and the invocation of emotion and cognitive effort is topographically indistinct (Nielsen, Balslev, & Hansen, 2005). Together with regions of the dmPFC, the pCC has been proposed to invoke episodic traces in the service of retrospective memory or prospective construction of scenarios (Buckner & Carroll, 2007; Schacter et al., 2007; Spreng & Grady, 2009; Spreng et al., 2008). Because the neutral stimuli in our study also engages these episodic traces, simulation alone does not account for the greater activation for emotional stories. Similarly, the vmPFC has been implicated in discourse processing (Ferstl & von Cramon, 2002) and in processing emotional words (Beauregard et al., 1997; Maddock et al., 2003; Maratos et al., 2001), higher level inferencing of emotional discourse (Beaucousin et al., 2007; Corradi-Dell'Acqua et al., 2014; Ferstl et al., 2005) as well as self-referential processes and reasoning about another person's thoughts (Ferstl & von Cramon, 2002; Frith & Frith, 1999; Gallagher & Frith, 2003).

The negative stories differentially engaged the bilateral TPJ, ATL, and STS all of which are regions that show relative overlap between narrative processing and mentalizing (ToM). Bilateral posterior temporal/parietal (TPJ) regions were significantly more active for stories eliciting emotional inferences compared to stories eliciting inferences about bodily states. These findings

are consistent with a role for this region in narrative comprehension as well as inferences of others' mental or emotion state above and beyond narrative comprehension alone (Beaucousin et al., 2007; Deen et al., 2015; Mar, 2011; Saxe & Kanwisher, 2003; Saxe & Powell, 2006). While our results are at odds with others who have shown that TPJ activation is related to mental/belief states but not emotional states (Mason et al., 2008; Zaitchik et al., 2011), the fact that negative scenarios had greater activation than even positive suggests that this region is not only responsive to emotion, but also to valence. This is consistent with recent findings from Bruneau et al (2012) who found greater activation to emotionally painful stories relative to non-painful (yet emotional) stories.

Negatively valent stories engaged the anterior temporal lobes (aTL) bilaterally to a greater extent than positive stories. In studies of discourse processing, there is strong evidence for involvement of the aTLs for language comprehension in general (Ferstl & Neumann, 2008), and more specifically for semantic integration over sentences and texts (see Stowe, Haverkort, & Zwarts, 2005 for review). However, findings of emotional valence in the aTL have not been documented previously. Other lines of research implicate the aTL for ToM processes (Frith & Frith, 2003; Gallagher & Frith, 2003) and for making inferences about others' emotional state (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Maratos et al., 2001; Völlm et al., 2006). In fact, Völlm and colleagues (2006) showed overlapping areas of activation in aTLs for empathy and theory of mind tasks. A recent review proffers the suggestion that the aTL are, "sensitive to stimuli that tell a story. . .and to tasks that require one to analyze other agent's emotions, intentions or beliefs" (Olson & Plotzker, 2007). Our data are consistent with past findings and extend them to demonstrate that aTL plays a role in making emotional inferences from sentence

context without explicit lexical reference to the emotion. This effect appears to be enhanced for negatively valent stimuli. Thus, like dmPFC and TPJ, the aTL likely plays a role in the evaluation of emotionally-relevant mental states conveyed through linguistic stimuli beyond the semantic information.

Decision Making Evokes Subcortical Brain Response

Based on previous studies of processing emotion in language (Beaucousin et al., 2007; Ferstl et al., 2005), we hypothesized that the amygdala would be involved in the inferential process for emotional scenarios. While we did not see subcortical activity in the amygdala and striatum during the story phase, this region was engaged in the context of the true/false congruency judgment including the putamen, caudate, insula and amygdala (see Figure 5 and Appendix D, Table 2). This is consistent with research that has shown the striatum is centrally involved in decision-making processes (Balleine, Delgado, & Hikosaka, 2007), particularly those involving a social component (Rilling et al., 2002; Sanfey, 2007). Emotional processes also play a role in decision-making (Grecucci, Giorgetta, van't Wout, Bonini, & Sanfey, 2013; Naqvi, Shiv, & Bechara, 2006). This may explain why, in contrast to previous studies of emotional words (Maddock et al., 2003; Maratos et al., 2001; Nakic et al., 2006; Straube et al., 2011) and stories (Beaucousin et al., 2007; Ferstl et al., 2005), our emotional vignettes failed to elicit amygdala activations. Each of these studies included a) explicit references to emotion or b) a response condition, suggesting that previous findings were due to decision making factors on emotion (Pérez-Edgar et al., 2007).

CONCLUSION

The present study extends previous research on inferential processing of emotional language (Beaucousin et al., 2007; Bruneau et al., 2013; Bruneau et al., 2012; Ferstl et al., 2005; Ferstl &

von Cramon, 2007) by differentiating positive and negative emotion, and also by examining the BOLD response to vignettes separately from the response condition. We showed that verbal emotional stimuli enhances activation of cortical regions generally responsive to discourse, and also regions associated with affective processing and social cognition, specifically medial and orbital frontal regions, bilateral middle temporal areas, temporal parietal junction/superior temporal gyri and pCC/PC. We also showed that these regions respond differentially to positive and negative valence, for example in the medial frontal region where activation was more dorsal for negative stories and ventral for the positive condition. The findings of the present study also suggest that mentalizing alone does not account for the differences between emotional and neutral stories, as all of our emotional stories required similar inferencing of the feelings of the protagonist. Finally, our results for the judgment task showed striatal and amygdala activations, whereas we failed to show similar activations for stories, suggesting the importance of decision making factors on emotional processes.

Table 1. Sample scenarios for pilot study

Condition	Scenario
Negative	The woman could not get over the idea that her ex-boyfriend did not want to be with her anymore. Hearing that he was dating someone new made the situation even worse.
Positive	The young man had waited so long for his favorite band to come to town that he could hardly sleep the night before the concert. He planned to arrive early to get autographs.
PhyState	After the race, the jockey was covered head to toe, and he couldn't see through his goggles. Days of rain had saturated the track, so the horses kicked up great clods as they ran.

Note. A total of 108 sentences were constructed, 36 each negative-, positive- and physical state. Emotional- or physical state was implied.

Table 2. Behavioral results

	Response time in msec		Accuracy % correct	
Condition	Mean (SD)	Standard error	Mean (SD)	Standard error
PosCon	1164.67 (280.66)	62.72	98.75 (3.35)	.75
PosIncon	1228.31 (297.88)	66.61	98.74 (2.40)	.54
NegCon	1316.06 (243.86)	51.21	96.65 (5.18)	1.16
NegIncon	1320.83 (303.28)	67.82	96.45 (4.14)	.93
NeutCon	1351.70 (330.08)	73.83	97.48 (3.94)	.88
NeutIncon	1570.82 (309.98)	69.11	95.40 (6.33)	1.42

Note. Response time (RT) and accuracy results. 72 stories were distributed over 3 conditions of valence (36 positive, negative and neutral) and congruency (18 congruent and incongruent. Values are reported as mean, standard deviation (*SD*) and standard error. RTs are reported in milliseconds.

Table 3. Brain activity associated with emotion and neutral scenarios

	Left					Right				
Region label	*x*	*y*	*z*	*t*	*d*	*x*	*Y*	*z*	*t*	*d*
Emotion > Neutral										
Frontal										
vmPFC	-2	38	-22	7.48	3.16					
	-4	42	-20	7.17	2.67					
dmPFC	-10	54	38	8.73	4.00	6	52	20	7.65	3.51
	-8	56	22	7.92	3.63	4	50	44	6.74	3.09
	-2	58	36	6.52	2.99					
	-4	60	10	6.40	2.94					
Temporal										
STS	-60	-16	-6	8.62	3.95	52	-6	-12	7.65	3.51
MTG	-54	-12	-12	9.91	4.55	58	-18	-10	10.24	4.70
	-52	-2	-26	8.82	4.05	64	-10	-18	9.03	4.14
	-52	-20	-12	8.56	3.93	48	-34	0	8.76	4.02
	-56	-2	-24	8.55	3.92	56	-38	0	8.41	3.86
	-52	-36	-2	7.95	3.65	58	-34	-2	8.25	3.79
	-50	-6	-20	7.71	3.54	50	-6	-20	8.23	3.78
	-64	-16	-14	7.67	3.52	50	-2	-22	8.12	3.73
	-56	-30	-6	6.69	3.07	58	-36	-8	7.86	3.61
						58	4	-26	7.58	3.48
						50	4	-22	7.56	3.47
						58	-4	-10	7.36	3.38
						52	-60	24	6.23	2.86
Middle temporal pole	-54	8	-30	9.05	4.15	46	12	-28	7.98	3.66
						46	20	-28	7.06	3.24
ITG	-50	0	-30	8.04	3.69					
Parietal										
Supramarginal gyrus						62	-54	26	6.39	2.93
Angular gyrus	-60	-60	28	8.84	4.06	56	-62	32	6.46	2.96
	-42	-58	28	8.80	4.04					
	-48	-60	32	8.70	3.99					
Subcortical										
aCC	-4	52	20	8.18	3.75					
	-8	50	18	7.98	3.66					
mCC	-2	-52	34	10.22	4.69					
Precuneus	-2	-58	26	7.55	3.46					
Cerebellum										
Cerebellum crus I	-20	-76	-34	8.21	3.77					
	-20	-82	-28	7.17	3.29					
Cerebellum crus II	-28	-80	-34	7.48	3.43	24	-76	-34	6.72	3.09
	-16	-84	-36	6.46	2.97					
Neutral > Emotion										
Frontal										
vmPFC	-22	32	-16	9.42	4.32					
IFG (tri)	-42	36	14	8.23	3.78					
Parietal										
Supramarginal gyrus	-64	-28	28	7.5	3.44					
	-60	-32	44	6.2	2.84					

Note. We show *t*-values for signal increases associated with emotion using Positive + Negative vs.

Neutral, signal increases associated with neutral using Neutral vs. Positive + Negative. Coordinates are MNI space. Height threshold: $t = 6.14$, $P < .05$, FWE corrected. Extent threshold: $k = 0$ voxels.

Table 4. Brain activity associated with valence

Region label	Left					Right				
	x	*y*	*z*	*t*	*d*	*x*	*y*	*z*	*t*	*d*
Negative > Neutral										
Frontal										
vmPFC	-2	40	-22	6.29	2.04					
dmPFC	-4	52	22	8.40	2.73	6	52	20	8.09	2.62
	-2	46	32	6.53	2.12	6	50	42	7.0	2.27
	-2	58	36	6.29	2.04	6	42	36	6.47	2.10
mPFC	-10	54	38	8.27	2.68					
IFG						48	32	-10	6.33	2.05
Temporal										
STS	-42	-58	28	8.58	2.78					
	-68	-50	20	6.70	2.17					
	-68	-44	4	7.07	2.29					
	-44	14	-22	6.92	2.25					
MTG	-54	8	-30	10.29	3.34	52	-22	-12	11.37	3.69
	-54	-12	-12	10.03	3.25	58	-18	-10	10.85	3.52
	-54	-36	-2	9.55	3.10	48	-34	0	9.64	3.13
	-52	-2	-26	9.30	3.02	56	-34	-4	9.33	3.03
	-52	-22	-10	9.06	2.94	50	6	-22	9.11	2.96
	-58	-30	-6	8.43	2.74	58	-38	0	8.96	2.91
	-60	-16	-6	8.21	2.66	50	-2	-22	8.87	2.88
	-54	2	-18	7.83	2.54	64	-14	-16	8.38	2.72
	-46	-42	0	7.20	2.36	54	-6	-12	8.21	2.66
	-68	-44	4	7.07	2.29	54	-4	-10	8.16	2.65
	-64	-16	-14	6.64	2.15	52	-30	-8	8.07	2.62
						48	6	-30	7.96	2.58
						56	6	-26	7.89	2.56
						60	2	-14	7.87	2.55
Middle temporal pole	-60	6	-16	6.75	2.19	46	12	-28	9.23	2.99
						48	18	-26	8.24	2.67
Parietal										
Inferior parietal						52	-46	28	6.38	2.07
Angular gyrus	-60	-60	28	9.58	3.12	56	-62	32	7.10	2.30
	-48	-58	30	8.65	2.81	62	-54	32	6.86	2.23
						44	-50	24	6.68	2.17
Subcortical										
Precuneus	-4	-54	34	7.79	2.53					
Cerebellum										
Cerebellum lob VIIa crus I	-20	-76	-34	9.23	2.99	24	-82	-30	7.22	2.34
	-20	-82	-28	7.71	2.50	26	-76	-34	7.15	2.32
Neutral > Negative										
Frontal										
vmPFC	-22	34	-16	9.05	2.94					
IFG (tri)	-40	36	14	8.08	2.62					
Parietal										
Supramarginal gyrus	-64	-28	28	7.25	2.35					
	-60	-32	44	6.83	2.22					
	-54	-30	40	6.34	2.06					
Positive > Neutral										
Frontal										
vmPFC	-6	46	-4	6.29	2.04					
	-4	38	-22	6.27	2.03					
dmPFC	-10	54	38	7.0	2.27					

	-4	60	10	6.86	2.23				
	-8	56	22	6.81	2.21				
	-10	52	20	6.59	2.14				
Temporal									
MTG	-52	-14	-16	7.57	2.46	64	-10	-18	8.14
	-60	-14	-8	6.89	2.24	58	-18	-10	6.99
	-64	-16	-14	6.83	2.22	44	-44	4	6.61
	-56	-2	-24	6.80	2.21	50	-6	-20	6.17
Parietal									
Angular gyrus	-42	-58	28	6.81	2.21				
	-46	-60	32	6.77	2.20				
Subcortical									
pCC	-2	-50	32	10.76	3.49				
	-2	-46	30	10.48	3.40				
Precuneus	-2	-58	26	7.64	2.48				
Neutral > Positive									
Frontal									
vmPFC	-22	32	-16	7.70	2.50				
IFG (tri)	-42	36	14	6.53	2.12				
Negative > Positive									
Temporal									
MTG	-56	-34	-4	6.69	2.17	52	8	-20	6.3
Positive > Negative									
Subcortical									
Cuneous	-12	-72	34	6.77	2.20				
mCC						8	-30	32	6.16

Note. We show *t*-values for signal increases associated with valence using four contrasts from repeated measures ANOVA: Negative vs. Neutral, Neutral vs. Negative, Positive vs. Neutral, Neutral vs. Positive, Negative vs. Positive and Positive vs. Negative. Coordinates are MNI space. Height threshold: t = 6.14, P < .05, FWE corrected. Extent threshold: k = 0 voxels.

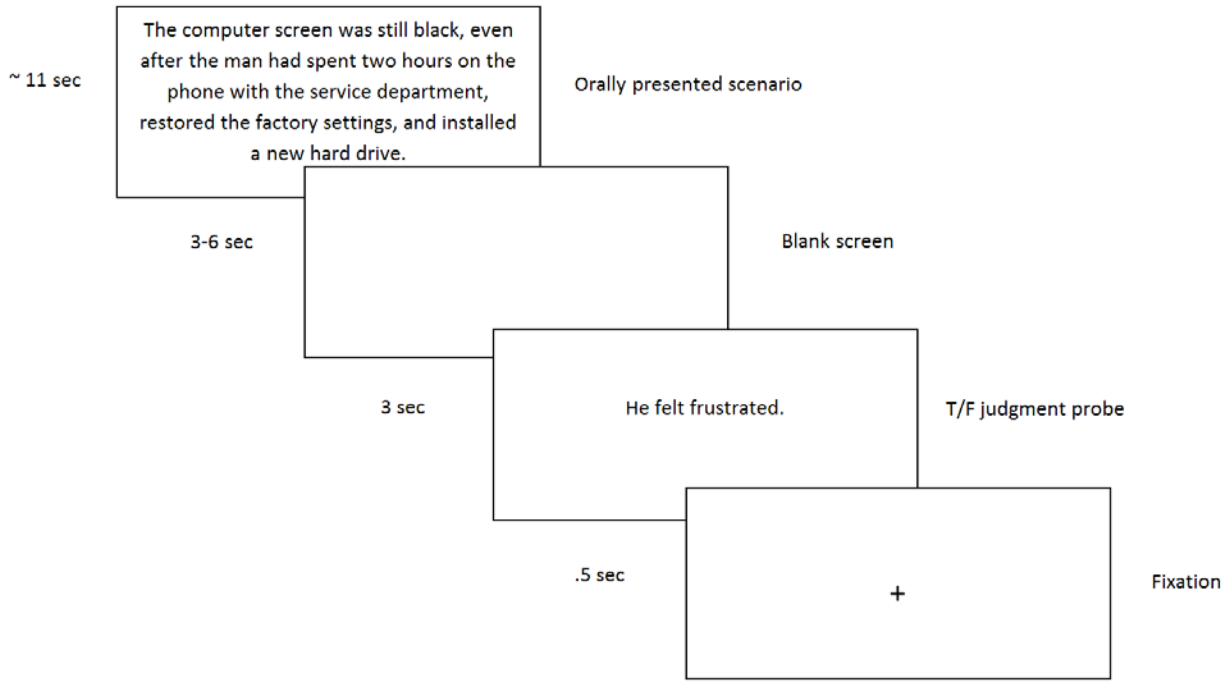

Figure 1. Experimental Design. 72 passages (24 each positive, negative, physical state) and a congruent and incongruent Target sentence were evenly distributed over 4 runs using an event-related paradigm. Congruent and incongruent items were randomized. Each run began with the display of a fixation cross for 500 msec, followed by the aurally-presented passage (~10-12 seconds). A blank screen followed for a duration that was jittered between 3-6 seconds. Then, the Target sentence "*He/She felt* …" with a congruent or incongruent word was presented visually for 3 seconds during which T/F judgment was made via a button press. Each trial was presented for 16-18 sec; inter-trial interval jittered 3-5 sec.

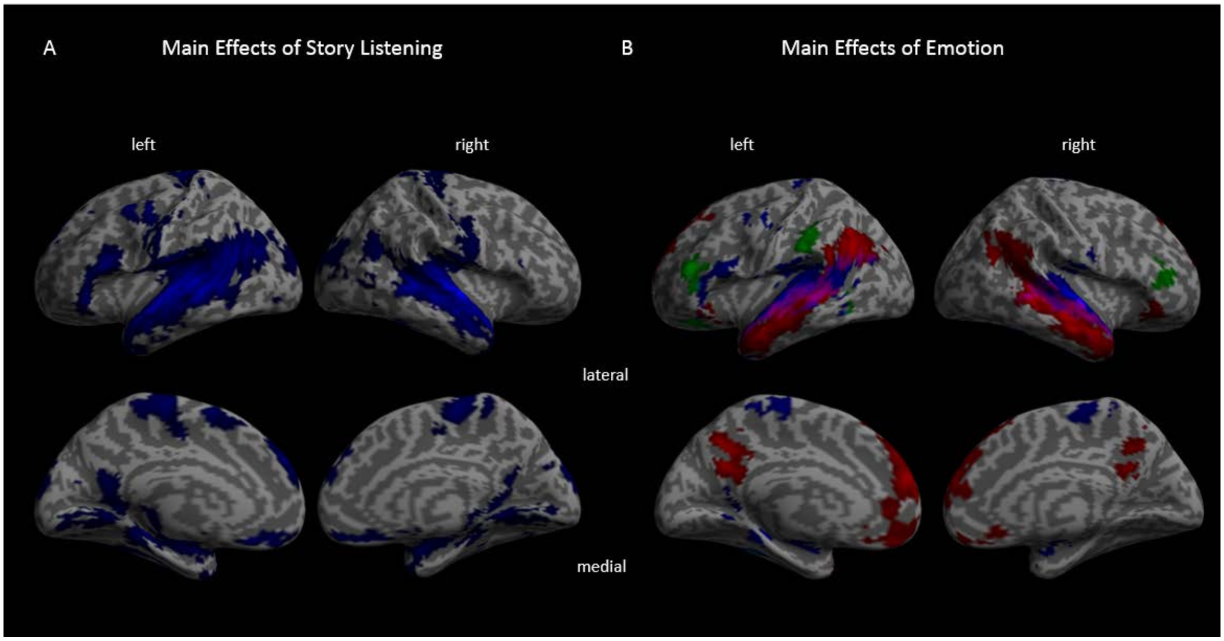

Figure 2. Activation maps illustrating the presence of significant functional activity associated with listening to stories. A) Positive BOLD activation for all stories (the average effect of positive + negative + neutral; blue). B) Activation associated with effect of emotion (positive + negative) > neutral, red; neutral > emotion, green; neutral < baseline blue; overlap, purple. Regional variations in task-related activity are displayed using a threshold of $p < .001$ corrected with cluster extent FWE threshold ($p < .05$) for t-statistic maps.

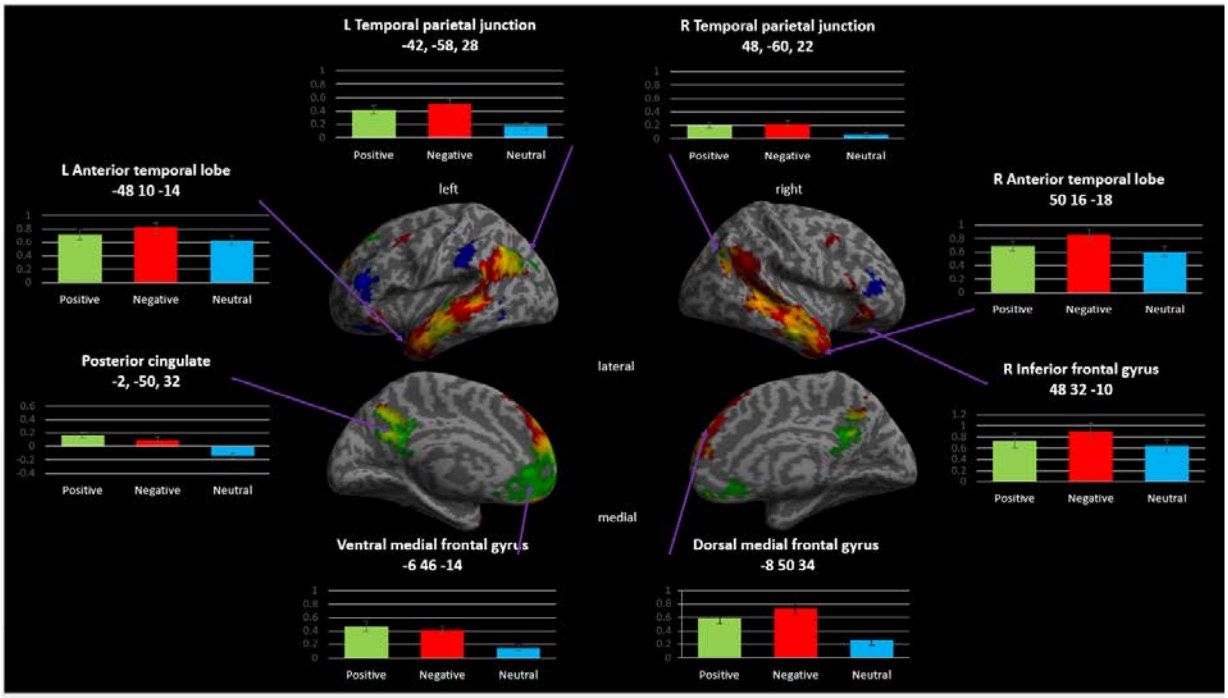

Figure 3. Activation maps illustrating the presence of significant functional activity associated with valence; effect of positive vs. neutral is shown in green, negative vs. neutral is shown in red, and neutral vs. emotion (positive + negative) is shown in blue. Yellow indicates areas of overlap. Regional variations in task-related activity are displayed using a threshold of $p < .001$ cluster corrected for t-statistic maps. Error bars show standard error.

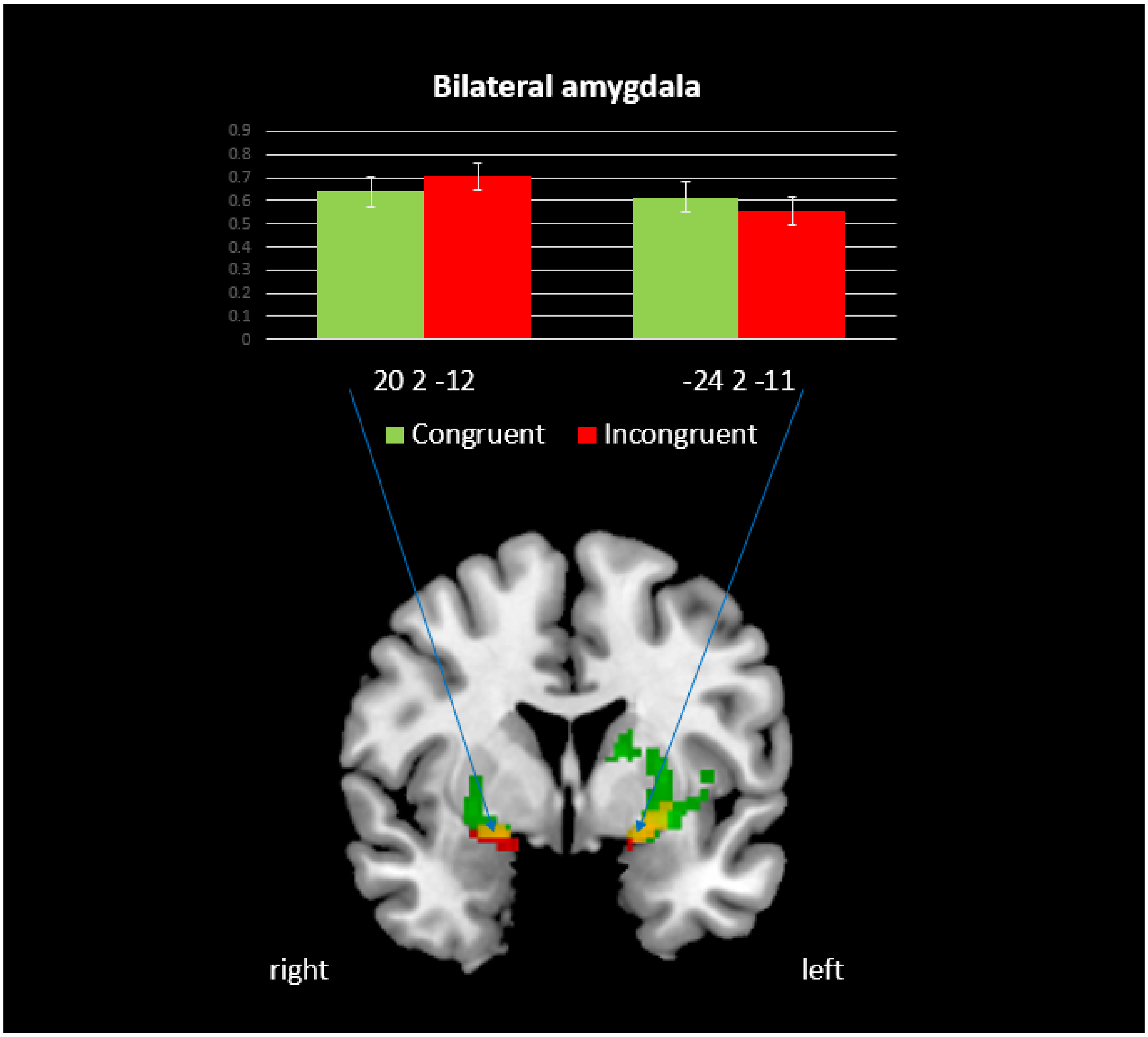

Figure 4. T/F response results. Activation maps illustrating the presence of significant functional activity in subcortical areas associated with probe; effect of CON is shown in green, INCON is shown in red; areas of overlap are yellow. Regional variations in task-related activity are displayed using a corrected threshold of $p < .05$ FWE for t-statistic maps.

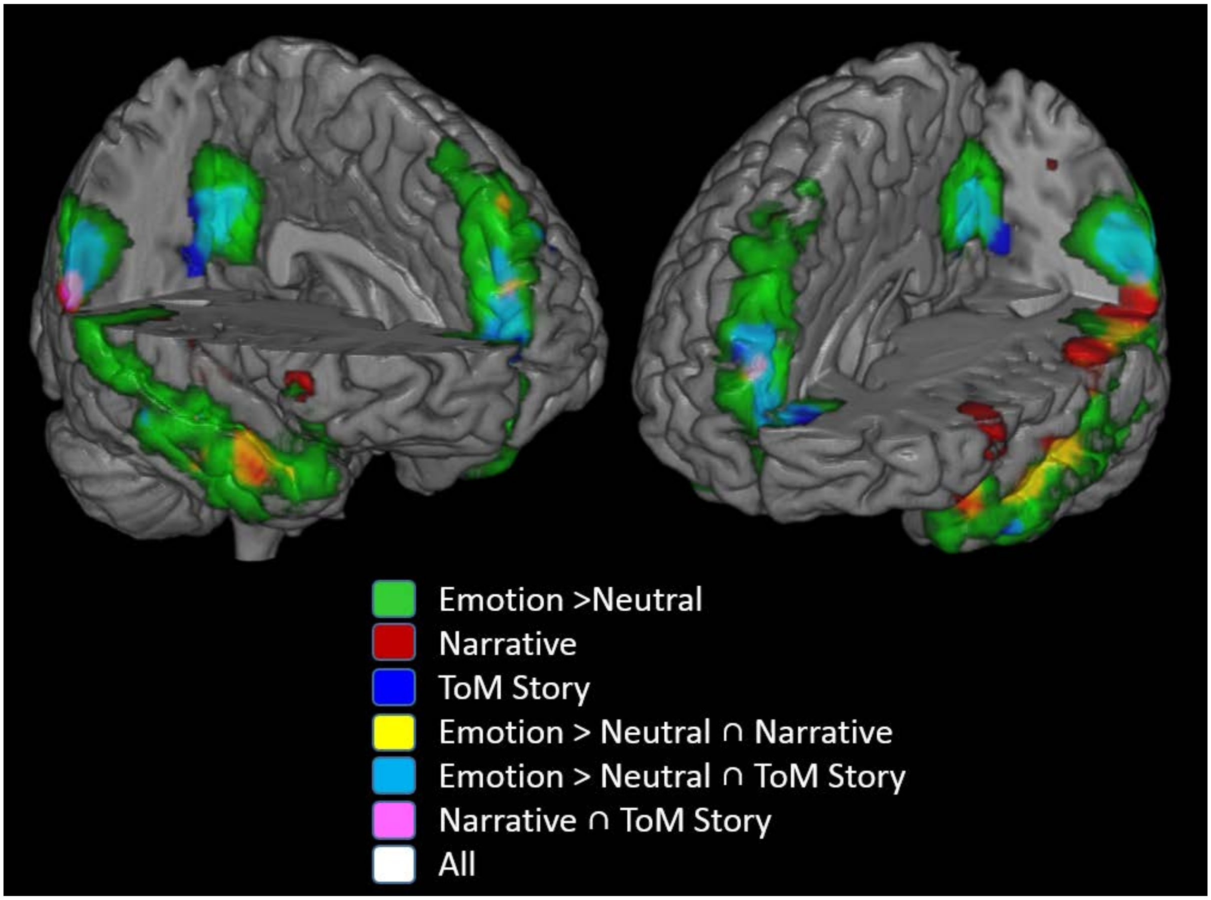

Figure 5. Emotion (EMO) > neutral (NEUT) activation (green) shown together with regions associated with narrative comprehension (NARR; Mar, 2011; red), ToM stories (TOM; Mar, 2011; dark blue), areas where (EMO > NEUT) ∩ NARR (yellow), (EMO > NEUT) ∩ TOM (light blue), NARR ∩ TOM (pink) and the overlap of all (white). Regional variations in task-related activity are displayed using a threshold of *p*<.001 corrected with cluster extent FWE threshold (p<0.05) for t-statistic maps.

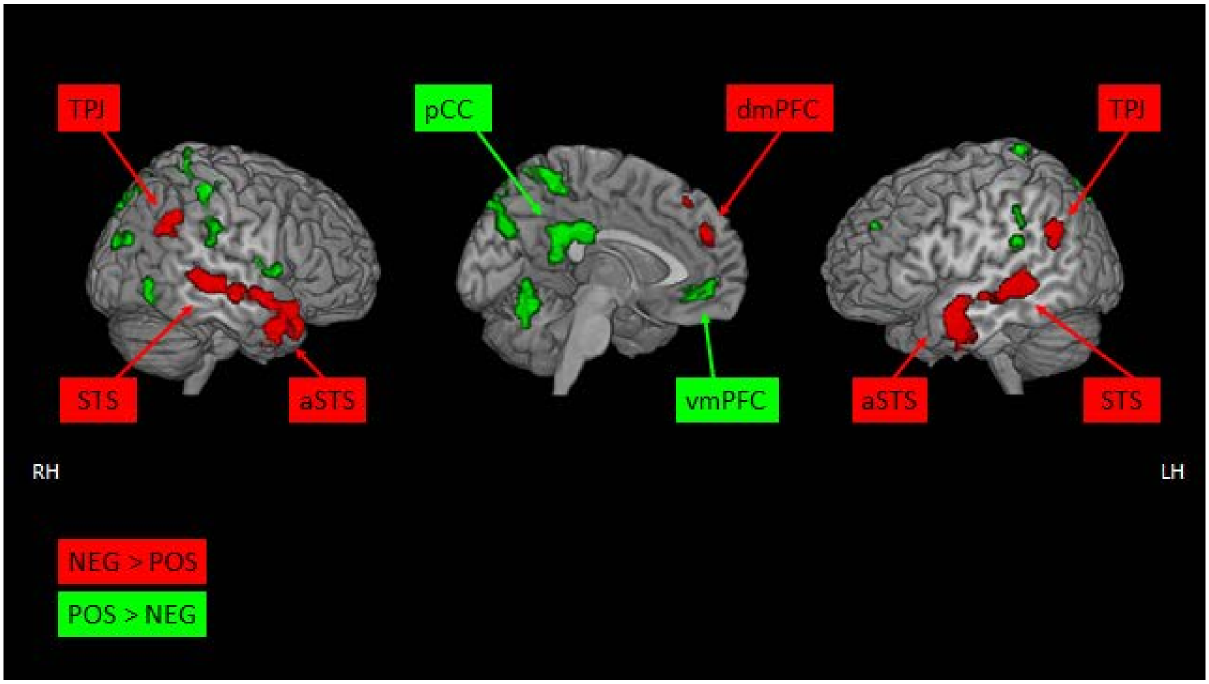

Figure 6. Contrasts of negative compared to positive (NEG > POS; red) and POS > NEG (green). Regional variations in task-related activity are displayed using a threshold of $p <$ .001 corrected with cluster extent FWE threshold ($p<0.05$) for t-statistic maps.

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